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THE ROYAL SOCIETY
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WESTERN AUSTRALIA, INC.

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1946 - 1947



The Authors of Papers are alone responsible for the statements
and
the opinions expressed therein.

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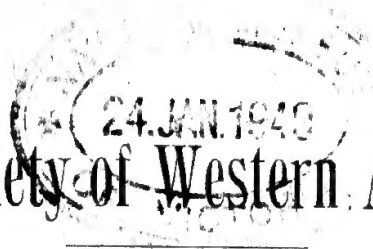
1948

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The Royal Society of Western Australia (Inc.)

ANNUAL REPORT OF THE COUNCIL FOR THE YEAR ENDING 30th JUNE, 1947.

Ladies and Gentlemen,

Your Council begs to submit the following report for the year ending 30th June, 1947.

Council.—Early in the period under review, Council decided to revert to the pre-war system of regular monthly meetings of the full Council. There have been, therefore seven regular Monthly Meetings and two Special Meetings of Council while the Executive met as such only twice.

Towards the close of this financial year, our President, Dr. A. G. Nicholls, received an appointment with the Council for Scientific and Industrial Research in New South Wales. In consequence, our senior Vice-President, Mr. J. Shearer, has conducted the affairs of the Society for the remainder of the year.

Dr. Teakle also has left this State, having been appointed to the Chair of Agriculture at the University of Queensland. The vacancy on the Council consequent upon Dr. Teakle's resignation therefrom was filled by Mr. A. C. Shedley.

Finance.—It is with gratification we record the successful conclusion of the protracted negotiations for an increase in the Annual Grant from the Government. Our Government has agreed to increase the Annual Grant to Two Hundred Pounds per annum, commencing from the First of July, 1946. As additional assistance for this financial year, the Government will agree also to the Government Printer printing our 1945-46 Journal without cost to the Society.

Membership.—The total membership of the Society at the conclusion of the year is very little different from last year. Membership of the Society, which now numbers 189, is made up as follows:

Honorary Members	6
Life Members	2
Corresponding Members	7
Ordinary Members	129
Associate Members	27
Student Members	18

The names of twelve Ordinary and two Associate Members were added during the year. The current Student Membership is the same as for the calendar year of 1946. Eight Ordinary Members and four Associate Members have resigned.

It is with regret that we record the death of three of our Members. Mrs. A. M. Bird, of the Old Farm, Albany, who had been an Honorary

Member of this Society for many years, passed away early in September, 1946. The Rev. R. B. Love, of Ernabella Bisison, via Oodnadatta, South Australia, left this sphere of service to humanity during the year. Mr. R. W. Fletcher, late Director of the Kalgoorlie School of Mines, died while a comparatively young man.

Journal.—At the last Annual Meeting we reported that Volume XXXI, 1944/45 of our Journal was in the hands of the Government Printer. Because of the pressure of official printing, this volume has been held at the galley-proof stage for many months, but its issue is now expected at an early date. The Honorary Editor is holding Volume XXXII, 1945/46, in manuscript form until the Government Printer has completed Volume XXXI.

In an endeavour to rectify the position as regards the publication of our Journal, a commencement has been made on the printing of Volume XXXIII, 1946/47 at the printing house of Pilpel & Co. It is probable, therefore, that the volume for the year just ended will be issued before that for 1945/46.

Library.—Normal exchange relations with numerous overseas and Australian institutions continue. We are pleased to be able to report that this Society has entered into exchange relations with two additional institutions, namely, the Department of Geology and Palaeontology, University of St. Paul, St. Paul, Brazil, and the University of Hawaii, Territory of Hawaii.

Exchange relations with three overseas institutions, interrupted for many years by the recent conflict, have been resumed during the past twelve months. Journals published during the war and held over for dispatch at the close of hostilities, have now been distributed.

J. SHEARER,
Vice-President,
acting for President.

S. E. TERRILL,

G. E. MARSHALL,
Joint Hon. Secretaries.

ABSTRACT OF PROCEEDINGS, 1946-47

9th July, 1946:

Annual Meeting in Gledden Hall.

Presidential Address: "Biological Control in Western Australia"; by Mr. C. F. H. Jenkins.

13th August, 1946:

Addresses: (1) "Biology of a Coccid parasite on the Tuart," by Mr. J. Short.

(2) "The Tuart and its environment," by Mr. C. A. Gardner.

Election: Mr. O. I. Kee Hock, Mr. J. R. Clark, Dr. S. E. Williams, Mrs. H. C. Williams, Mr. J. F. Ivanac, Miss J. C. Kahan, and Mr. E. C. Hodgson, as Ordinary Members.

10th September, 1946:

Address: "Diseases Associated with Vitamin B Deficiency," by Dr. Bruce Hunt.

Election: Mr. E. P. Hodgkins, as an Ordinary Member; Miss H. E. Cook, as an Associate Member.

8th October, 1946:

Paper: "The influence of Wind on the Geomorphology of the Pelsart Group of Abrolhos Islands," by Dr. R. W. Fairbridge.

Address: "Ultrasonics," by J. Shearer.

12th November, 1946:

Meeting cancelled due to Railway strike and resulting electric power shortage.

10th December, 1946:

Paper: "Two new Minerals from Londonderry," by Messrs. H. P. Rowledge and J. D. Hayton.

Symposium: "Agar Agar."

Election: Mr. H. T. Phillips, as an Ordinary Member.

11th March, 1947:

Paper: "A Grazing incidence method for the Determination of High Refractive Indices," by Mr. S. E. Terrill.

Address: "Some aspects of classification of Properties for Settlement Purposes," by Mr. W. V. Fyfe.

Election: Miss P. Kott, as an Ordinary Member.

8th April, 1947:

Address: "Endemic filariasis in Malaya," by Mr. E. P. Hodgkin.

Election: Mr. A. C. Ramm, Mrs. A. C. Ramm, and Mr. P. J. Kenny, as Ordinary Members.

13th May, 1947:

Address: "Weather forecasting as applied to Fire Control," by Mr. W. R. Wallace.

10th June, 1947:

Paper: "The Anatomy of the Quokka, *Setonix brachyurus*, Part I, External Morphology of the large Intestine," by Mr. J. R. Clarke.

Address: "Modern Methods of Oil Prospecting," by Mr. A. Reid, supported by films by courtesy of the Shell Oil Co.

THE ROYAL SOCIETY OF WESTERN AUSTRALIA, INCORPORATED.

STATEMENT OF RECEIPTS AND EXPENDITURE FOR THE YEAR ENDED 30th JUNE, 1947.

RECEIPTS.			EXPENDITURE.		
General Fund—					
Balance at 30th June, 1946	£	s. d.	Petty cash, postage, etc.	£	s. d.
Cash in hand, 30th June, 1946	188	3 3	Clerical assistance	31	17 8½
Subscriptions, current and arrears	1	2 0	Rent—Jan. to June, 1946	6	11 6
paid in advance	130	9 9	July, 1946, to June, 1947	15	0 0
	5	12 10	Meetings—Catering	45	0 0
Government Grant	136	2 7	Annual Meeting	13	8 0
Interest: Current account	199	19 11	Government Printer:	4	12 6
War Loan, 1959			Volume 30	153	10 9
Authors' reprints and half cost of blocks	4	5 5	Other printing	5	12 5
Sale of Journals	31	13 9	Honorarium, Editor	159	3 2
Other receipts	5	5 0	Subscriptions	15	15 0
	1	10	Other payments	13	7 4
			Cash at Bank, 30th June, 1947	289	1 2
			Unpresented cheques	14	1 4
			Cash in hand, 30th June, 1947	£274	19 10
			Unbanked cheque	1	1 6½
				10	8
				276	12 0½
				£566	13 9
Medal Fund—					
Balance at 30th June, 1946	£	s. d.	Balance—Cash at Bank, 30th June, 1947	£	s. d.
Interest	11	16 2		12	0 6
	4	4		£12	0 6
	£12	0 6			

Endowment Fund—			£ s. d.			£ s. d.		
Balance at 30th June, 1946				
Interest—				
War Savings Certificates				
War Loan, 1956				
Bank account, 1947				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
				
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JOURNAL OF THE ROYAL SOCIETY OF WESTERN AUSTRALIA.

VOLUME XXXIII

1.—NOTES ON THE GEOMORPHOLOGY OF THE PELSART GROUP OF THE HOUTMAN'S ABROLHOS ISLANDS.

By
RHODES W. FAIRBRIDGE, B.A., D.Sc., F.G.S.
Read: 8th October, 1946.

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I. INTRODUCTION.

(a) SCOPE.

My visit to the Abrolhos Islands came during the winter season, July, 1946, and most of the time was spent cruising in the great Pelsart lagoon, landing at one island or another and making reconnaissance surveys. Air photographs by the Royal Australian Air Force are only available for Pelsart Island itself (called on the photos "Batavia Road Island," K.D.1028, numbers V.1772-1805, 9-12-43, 5-inch lens, 4,400 ft.), and for Gun Island (numbers V.1808-1809, same data as above). The only chart is a rather inadequate one of ancient vintage by the British Admiralty, called "The Houtman Rocks" (No. 1723), and on a scale of about 3½ nautical miles to the inch.

Thus, although this material was all very valuable, I was forced to rely to a large extent on my own instrumental surveys. These were carried out by prismatic compass with pacing, a sufficiently accurate method for the size of islands involved. Elevations were measured by the eye-to-horizon method recommended by Kuenen (1933) for such coral island work; a check on this method, when used in appropriate areas, shows an error of much less than 1 in 10 feet.

In this way, sketch-maps were prepared of four of the islands in the Pelsart lagoon and other islands more superficially inspected. Three of these sketch-maps are reproduced herewith. (See text figs. 2, 4, 5.)

For some time I have been particularly interested in the influence of winds and wind-induced currents in the shaping and development of coral reefs. This study has been particularly stimulated by the examination of aerial photographs of such reefs during the war in the South-West Pacific (see Steers, 1945). I was then in charge of an Intelligence research section of the Royal Australian Air Force, and in particular made a special investigation of coral reefs, by land, sea, and air, in company with Dr. Curt Teichert and Dr. (then Lt./Col.) F. W. Whitehouse. Photo interpretation is not merely a great aid in unravelling the problems of the surface features, the geomorphology of coral reefs and islands, but also sheds light on other physiographic matters, such as the nature of prevailing winds and wave action. The pattern of the waves, often in intersecting series, is most instructive in explaining the shape and growth of coral reefs.

In contrast to these mainly constructional aspects of reef physiography, I have paid special attention to the destructive factors which tend to counteract the former. These are classified as biological, mechanical and chemical, the greatest of all being chemical, and a preliminary attempt is made to explain the solution of coral limestone by sea water under certain physical and biological conditions.

Finally, I have been on the look-out for evidence of old sea-levels, which in such a highly stable region as Western Australia during the recent epoch we would expect to be truly eustatic, without danger of distortion by isostatic or other local causes. I was not surprised therefore to find old marine benches and similar evidence at precisely the same levels as I had already observed at many points along the mainland coast.

From these particular studies, and from a general review of the physiographic position of the Pelsart Group, aided by the aerial photographs, the Admiralty Chart, and the results of previous workers, I believe I have been able to draw certain conclusions of general applicability.

As regards names, I have followed those found in the Admiralty Chart. Unfortunately, many of the smaller islands are without names, though some have had names bestowed upon them by the fishermen. In this way we have Post Office Island (formerly used as a cache for mail collection), Coronation Islets, Nook Islet, etc., in the Mangrove Groups, and I have marked these on the map; others here are known temporarily after the fisherman, or his vessel, customarily based there,

e.g., Charlie's Islet, "Maori Lass" Islet, but as these appear to have no lasting validity, I have not included them.

On an old sketch-map preserved at the Lands Department, Perth, numbered O.P. Eng. 235, there are quite a number of these small islets with names. They include "Wreck Island" (at the south end of Pelsart Is., referred to by Teichert as "Little Island"), "Jubilee Island" (now known by fishermen as "Stick Island"), "Nought Island" (now known as "Green Island"), and a group of islets lying between Middle Island and Rat Island, numbered from "One" to "Eight." Only these latter have I incorporated in my map (see text fig. 1). There is also a "Post Office Island" on the Lands map, but this corresponds to what the fishermen at present call "the Nook" or "Nook Islet."

Grateful acknowledgment must be made to Mr. Keith Sheard, officer of the Division of Fisheries, of the Australian Council for Scientific and Industrial Research, who organised the trip, the success of which was largely due to his excellent companionship and his introduction to our able skipper, Mr. Jack Basedon, of the "Maori Lass." Expenses were defrayed by a university research grant from the Commonwealth Government. Skilled assistance with the drafting was provided by Mr. Henry Coley.

(b) PREVIOUS WORK.

Earlier workers have concentrated their attentions mainly on the biology of the reefs or on the geomorphology of the larger islands. Little or no work has been done hitherto on the smaller islands that dot parts of the Pelsart lagoon and fringe its northern border.

The Admiralty hydrographic surveyor, Captain Wickham, already over a century ago noticed the difference between the flat, tabular limestone of some of the islands in contrast to the loose coral detritus and shells of certain other islands (1841). Saville-Kent in his "Naturalist in Australia" (1897) made a notable contribution in his description of the growth of a coral island from an initial accumulation of such debris on a reef near Gun Island.

Dakin (1919) contributed a valuable general description of the islands and their reefs, classifying them, incidentally, as evolutionary steps on the way to becoming atolls. The latest work is by Teichert in his "Contributions to the Geology of Houtman's Abrolhos" (1947*a*), the results of his careful surveys there in 1944, some of which he was later able to interpret in the light of our joint experiences, both on the ground and in the air, in the Great Barrier Reef area in 1945.

This work of Teichert's is the first strictly geological and geomorphological study of the Abrolhos and is one of the most valuable and complete that has ever been accorded a group of coral islands. I shall, therefore, make many references to this pioneer study, and many of my own observations may now only be regarded as amplifying and confirming his own. It should be added, however, that I did not possess his detailed maps or complete manuscripts when I visited the islands, so that these observations were for the most part independent of his.

Another paper of Teichert's, on Rottneest Island (1947*b*), was also in the press at the time of my visit, and is now particularly valuable for correlation of eustatic levels.

Earlier references to the work of wind in controlling the geomorphology of coral reefs may be found in most of the classical works on coral reefs from Darwin (1842) onwards. Wood-Jones (1910) was a particularly clear exponent of this subject, following upon his experiences in the Cocos-Keeling Islands. More recent observations may be found in Umbgrove (1929) for the Java Sea area; in Kuenen (1933) for other parts of the East Indies; in Krempf (1929) for the South China Sea; and for the Great Barrier Reef area, in Stephenson, Tandy and Spender (1931), Spender (1930), Steers (1929, 1937, 1938), and in papers by Fairbridge and Teichert (in the press).

(c) WINDS.

On my visit to the Abrolhos in July, 1946, I was singularly fortunate in being able to observe the effects of wind from almost every quarter. During that period a regular series of cyclonic disturbances were crossing the south-western part of the continent. The normal south-westerly winds, which blow for much of the year in this region, would generally back steadily to south, south-east and east, when there would be a day or two of calm and sunshine with a slight land breeze. Then it would back quickly to north and blow a gale from the north-west for several days; and then the process would be repeated at longer or shorter intervals.

Normally speaking, it may be said that on the average the southerly is the prevailing wind. During the three or four summer months (December-March) when these latitudes are affected by the tail of the trade-wind belt, it blows very steadily and with considerable force, from practically due south to south-south-east (the "Southerly Buster"). Gales of considerable violence come from north-west in the winter season. Milder south-easterlies are fairly common in the autumn and while storms from the north-east are rare, they exert a considerable effect on the unprotected northern islets.

(d) TIDES.

Coastal geomorphologists are becoming more and more conscious of the importance of tides in the local control of physiographic features. At the 25th A.N.Z.A.A.S. Meeting at Adelaide in August, 1946, with E. D. Gill, I made a special appeal that tidal figures be always included in coastal geomorphological studies. It is thus most unfortunate that we do not possess the appropriate data for the Abrolhos.

The Admiralty chart records a spring tidal range of $2\frac{1}{2}$ feet. There have, however, been no really scientific measurement of tides in the islands at all, and this figure is most certainly too low. On Pelsart, Teichert estimated that the range would be over 3 feet. While at the Mangrove Islets in the northern part of the Pelsart group, I came to the conclusion that the spring range was very close to 3 feet 6 inches. This figure represents an actually observed spring range in July, 1946, and also coincides with the calculated figures based on physiographic levels (see below).

It would, of course, be extremely valuable if continuous tidal records could be obtained by a mechanical tide gauge. On the other hand, however, fairly close estimates of maximum spring range can be obtained in coral islands by the following indications:—

- (i) First, the lowest spring tides will drop to a few inches, and no more, below the growing coral colonies. A very large percentage of the contemporary reef-level does not vary more than 1 foot above or below the level of low-water springs. That precise level can generally be observed by the dead tips of the *Acropora* fans, which grow up high during periods of neap tides and then get killed down by exposure at springs (see Plate I, figs. 1, 3 and 4). In non-living reef areas it may be observed that low-water springs is the absolute base-level of subaerial erosion, and in certain protected places this can be quite accurately judged.
- (ii) Then secondly, the height of maximum tidal range can be observed in protected lagoonal areas by the blackening of the dead coral. Again, this is the maximum height for the sea-water corrosion of calcium carbonate. In protected areas, the maximum chemical erosion of the limestone will be exactly at mean sea-level. Teichert has also noted this correspondence between the deepest undercutting of the cliffs and mean sea-level.

It may be seen thus that our elevations are really of quite a high order of accuracy, within a very few inches, although not founded on instrumental records. It is not argued that this is perfectly satisfactory, but it is certainly of great value for work in the nature of a preliminary reconnaissance.

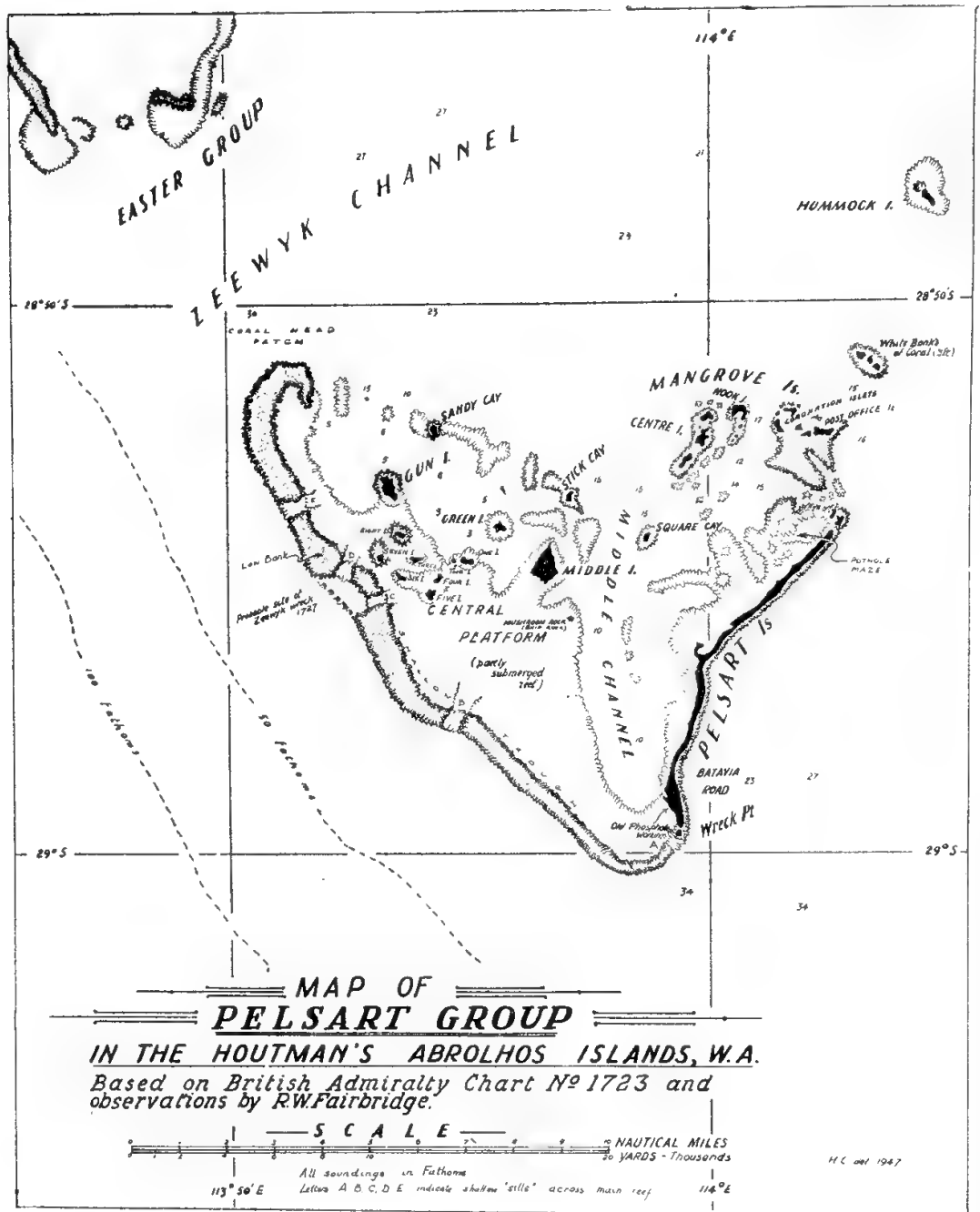
In this work I am following the usual Admiralty method of referring all heights to mean low springs as "datum." Advantages of this method I have already outlined (with E. D. Gill) at the 25th A.N.Z.A.A.S. Meeting (Adelaide, 1946).

The actual periodicity and time of tides is of no geomorphological significance, of course, but a few notes on the subject may be of practical value. Local enquiry showed that maximum spring tides, such as are best for examining coral reefs, occur generally in daylight in the months of June, July and August. They correspond then more or less with the lunar cycle. It is interesting to note that, while Dakin and Teichert found that from October to January the best low tide was generally in the early morning, I found in the opposite season that it was generally late in afternoon (varying from 3-6 p.m.). In any case, abnormalities are as frequent in this region as at Fremantle, where, as observed by Curlewis (1915), the lunar-controlled movements of the tide are often modified by the prevailing wind and barometric conditions.

II. OBSERVATIONS.

(a) THE BASEMENT.

The Pelsart, or Southern Group of the Abrolhos Islands is, according to both Dakin (1919) and Teichert (1947), the oldest and most mature of the Abrolhos reef complexes. It stands on a platform of about 25 fathoms depth, which connects it with the other islands and with



Text fig. 1. Map of Pelsart Group.

the mainland. It is possible, however, that the base of the coral may even be traced down to the 40 fathoms line. On the outer side, the south-western face of the group closely parallels, at a distance of 6-7 miles, the edge of the continental shelf, which hereabouts follows very approximately the 100-fathom contour (see text fig. 1). ⁽¹⁾

Superimposed on the south-western border of the 25-fathom platform, the Pelsart Group rises in a massive triangular block, sloping very steeply away to SW and SE, but much more gently to the north. A number of isolated reefs also rise from the 25-fathom platform in a north-easterly direction—the “Coral Patch” (“white banks of dead coral” of the Admiralty Chart), King Reef, Hummock Island (a sand cay 500 yards long and 16 feet high), Mid Reef and other lower patches where the swell may be seen breaking occasionally.

This massive coral reef platform is bounded by continuous reefs all along the south-west and south-east sides, and by scattered reefs and islets along the north side. The central lagoon is partially of deep water (10-15 fathoms) but is mostly blocked by reefs. The general impression is that of a *compound atoll*.

Darwin in his classical work “On the Structure and Distribution of Coral Reefs,” on the basis of Wickham’s survey, hesitated to class it as an atoll on account of the “extreme irregularity,” but as Dakin (1919, p. 177) has already pointed out, the Pelsart Group is far from irregular, and appeared to him to be an atoll. Teichert (1947, p. 191), on the other hand, held that this view is untenable owing to the presence of old reef cores. In my opinion, however, this feature is merely attendant on the long and variegated history of the Abrolhos and might perfectly well be associated with any reef which began as a simple atoll, but which experienced a similar complex evolution.

One could use Davis’ term “bank atoll” (1928, p. 19). Bank atolls, according to Davis, are “bank reefs, which rise back from the outer margin of rimless shoals.” If the reef is annular then it is a “bank atoll.” Clearly, Davis included the continental shelf in the “rimless shoal” category and therefore (*op. cit.*, p. 204) classified the Abrolhos as “a former bank atoll, uplifted and now in process of degradational transformation into a new sea-level atoll in the manner proposed by Agassiz (1899, p. 135).” Since Davis often used “bank” and “shelf” in the same sense, we might perhaps speak of it better as a “shelf atoll.” Teichert himself preferred to translate the Dutch “plaatrif” (of Niermeyer) as “shelf reef” (1947a, p. 191), and there is no doubt that this is clearer than any vague term using “bank” or “shoal.”

I should like to re-emphasise the fact that the Abrolhos reefs are not of the mid-Pacific type (where Darwinian subsidence appears to play a major rôle). Rather they are reefs built on stable foundations, and have suffered complex eustatic evolution. As Voeltzkow (1907) and

(1) Teichert noted irregularities in the soundings here, but it is clear that certain of the earlier soundings on the Admiralty Chart are badly misplaced, and in all probability the continental edge in front of the Pelsart Group seems to be nearly rectilinear in a NW-SE direction.

others have already observed for most of the Indian Ocean reefs, their cores do not consist of recent reef corals for the most part, but of various older lagoonal sediments and of old down-planed reef limestones, on which the contemporary corals grow "like flowers in a garden."

(b) THE SOUTH-WESTERN REEF.

On the south-west side, this approximately equilateral triangle is bounded by a typical ribbon reef of the barrier type, with symmetrically inwards curving extremities—the type which may be seen again and again over hundreds of miles along the outer edge of the northern section of the Great Barrier Reef of Queensland (see Stephenson, Tandy and Spender, 1931). The south-west barrier is 12 nautical miles in length, and over it the heavy south-west swell from the Indian Ocean may be seen continuously breaking. From a central point, such as Middle Island, which lies nearly 4 miles within the outer reef, it is possible to stand on a high tower and observe the wonderful spectacle of that wall of breakers and spray, rising continuously to 50 feet and more, through an arc of over 150° on the compass (see photograph, in Saville-Kent, 1897, p. 132). The width of the reef varies from one to several hundred yards, but the level is low, ranging from 1-5 feet, though it is sometimes possible to walk along sections of it at low tide, when the surf is not too great.

At certain points there are low shingle banks, as for example, opposite Gun Island, which rise a few feet above the general level. Scattered along the reef are dead coral boulders ("negro-heads") of various sizes. Many of these are loose and have merely been cast up by storms (the "jetsam" type described by Saville-Kent, 1893, and others), but others consist of old coral limestone *in situ* and with undercut margins which are obviously solution relics (as observed long ago by Dana and Agassiz, later by Gardiner (1931), and here in Pelsart Group by Teichert (1947a), proving once again that there are two sides to every argument!).

At high tide the sea pours over the outer reef at almost all points and sweeps into the lagoon. Dakin (1919) has compared it with a "huge natural weir." A maximum volume of water converges from west, south and east at the south-eastern extremity, pouring over a "sill" there, somewhat lower than the rest of the reef. Aerial photographs show how the newly abraded sedimentary debris is being washed from the outer edge of the reef here, northwards into the lagoon, where there is an ever-fresh cone of new sediment (see, for example, the air photo reproduced by Teichert, 1947a, Plate VII, fig. 1).

Mr. Keith Sheard, who has flown all along this south-western reef, has kindly informed me that there are no less than five of these "sills," even deeper than the southern one, distributed along the reef. Their position he has delineated on our map. The water pours over them, partly into channels on to and across the Central Platform and partly into a shallow trough or gutter around the inside margin of the reef (see text fig. 1).

This south-western barrier might appear to be a typical example of the characteristic product of a dominant swell and wind direction,

which on this coast is from the south-west. On the Great Barrier Reef, in contrast, the wind is dominantly south-east, but in that case the trend of these ribbon reefs are not at right-angles to the wind direction, and it may be concluded from the bathymetric evidence that the primary orientation of such reefs is due rather to the trend of the underlying shelf topography. As noted in the preceeding section, the south-western reef closely parallels the NW-SE trending shelf edge.

(c) THE SOUTH-EASTERN REEF AND PELSART ISLAND.

On the south-east side of the triangle there is a long sinuous island-capped reef, extending from the south-east "tail" of the outer barrier, away to the north-east for a distance of over 6 miles. This is Pelsart or Long Island (also called Batavia Road Island). It has a core of hard coral limestone rising to 18 feet above datum, and is superimposed by a complexity of younger deposits. (For a very complete description of the island, see Teichert, 1947a).

The island has no exact counterpart elsewhere in Australian waters, but may perhaps be compared with the raised margins of some of the larger Pacific atolls, of the Cocos-Keeling Group, or of compound atolls such as those of the Maldives, etc., in the Indian Ocean. The difference, of course, is that all those examples are situated on mid-ocean banks, while the Abrolhos rise from near the edge of a continental shelf.

This south-eastern face of the group is fully exposed to severe storms, but the main swell breaks along it after swinging about the southern extremity, around 90° from the south-west. In addition, the tail end of the south-east trades is felt here all through the summer. The controlling factor, however, is the south-westerly swell. Debris would have accumulated all along this south-eastern margin of the reef platform, but mostly just at the tail of the south-west barrier (about Wreck Point). From here the material would have been "shepherded" along to the north-east under the combined influence of the deflected waves of the south-westerly swell, breaking obliquely along the south-east side, and of the small waves, locally generated by the south-west wind within the lagoon, which would break obliquely along the north-east shore of the island. An analogous process has been observed in the building of long shingle tongues on the island reefs of the Great Barrier Reef lagoon.

(d) THE NORTHERN REEFS AND THE NORTHERN ISLETS.

Turning now to the third, or northern side of our triangle, we find a 10-mile sector of very irregular reef patches, both large and small, which in places are interfingered by a complicated network of deep channels (some exceeding 15 fathoms). These are coral reefs typical of fairly calm water conditions (Marshall, 1931). Many of them are crowned by small islets, some of fairly ancient origin, such as the Mangrove Islets, and others, such as Square Islet, Stick Islet, Sandy Islet etc. are merely shingle and sand cays of comparatively recent origin.

A study of the weather conditions quickly brings a partial explana-

tion for the irregularity of these reefs. For the greater part of the year this northern side is entirely protected from the southerly gales and from both the south-westerlies and south-easterlies. During the winter season, there are also storms of considerable violence from the north-west, and more rarely from the north-east. The force of the former may to some extent be broken by the presence of the Easter Group and the Wallaby Islands, which lie to the north-west. Nevertheless, at these times, as well as with westerly and south-westerly winds, a moderate swell is felt in the Zcewyk Channel and heavy surf may be seen along the northern edges of these reefs. The result is the accumulation of low shingle banks (not over 2 feet high) and small negro-heads (up to 3 feet only in diameter) along these northern rims.

Similar, but still lower shingle banks may be observed at low tide around the southern margins of those reef patches which are exposed to a few miles of "fetch" in the lagoon area. Even over such short distances a stiff gale may whip up sufficient waves to throw up fragments of the fragile coral species on to the reef edge (see Plate I, fig. 1). This is particularly well seen in the south and east of Stick Island.

Evidence from the plans of the old beach ridges of the Mangrove Islets etc. shows that at periods of higher sea-level these islets were less protected from the westerlies than at present, and high shingle banks were built up, with the typical incurving spits at each end which are so characteristic of shingle breastworks in the Great Barrier Reef and the Java Sea areas. True "ramparts" of asymmetric section are scarcely known, however.

An additional factor to wind, in the shaping of the northerly rim of reefs and islets, is that of tidal currents and scour. While the considerable irregularity in the detail of these reefs has been noted, a rough north-south orientation can be detected when viewed on the broad scale. This north-south alignment, by analogy with such cases as the Torres Straits reefs, may be interpreted as due to currents.

At the Pelsart Group it was observed that with the rising tide the current sets southward, into the lagoon through all the northern openings, while the falling tides sets to the north. These northern channels are the only exits for the whole lagoon, but especially at high tide a considerable body of water breaks over the twelve-mile section of reef in the south-west and enters the lagoon from that direction. This water tends to bank up with the rising tide, but augments the ebb tide very considerably, both in strength and duration. In this way a 2-3 knot northward current is often observable over extended periods at the northern openings.

Of all this evidence, none, however, appears to be adequate by itself to explain the obvious irregularity of the Northern Reefs, intersected as they are by 15-fathom channels. No such major breaks are found in the south-westerly and south-easterly reefs. These features appear to be beyond the control of the contemporary forces of growth and erosion, and thus we turn to events in the geological history of the group for the basic explanation (see Section III).

As noted above, the islets of the Northern Reefs are of two types, older ones of coral limestone material, and very recent ones of loose sand and shingle.

Of the former, let us take one of the *Mangrove Islets* as an example. These lie in the north-east part of the group and consist of about a dozen low islets, not more than 12 or 13 feet high, and 200 or 300 yards in length, and highly irregular in shape. They are all mainly of old coral limestone and surmounted by shingle beach ridges. They have little vegetation save for the mangrove patches that their name implies. In the west there is a group of three trending north-north-east, and for convenience I have called the middle one "*Centre Islet*" ($28^{\circ} 52\frac{1}{2}'$ S., $113^{\circ} 59\frac{1}{2}'$ E.).

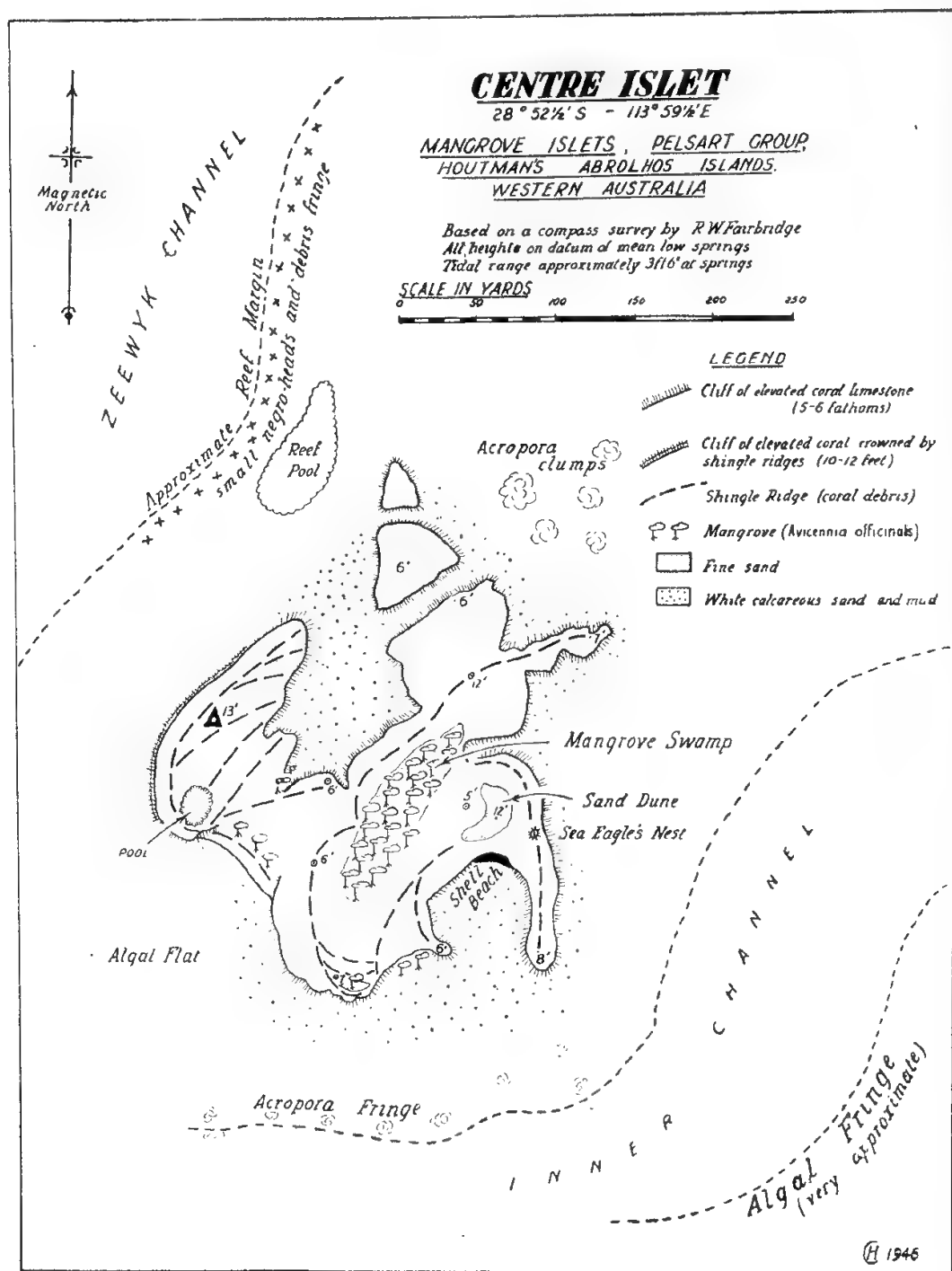
The islet is 300 yards long and an equal distance across, but with deep indentations so that its total area is not great (see text fig. 2). It consists fundamentally of a core of old coral limestone (mainly heavily branched *Acropora* species and coralline algæ) which stands in a uniformly cut platform at 5-6 feet above low-tide level. Most of its outline is marked by 5-foot cliffs of this rock. It is very hard and in many places the cliffs are deeply undercut by the sea.

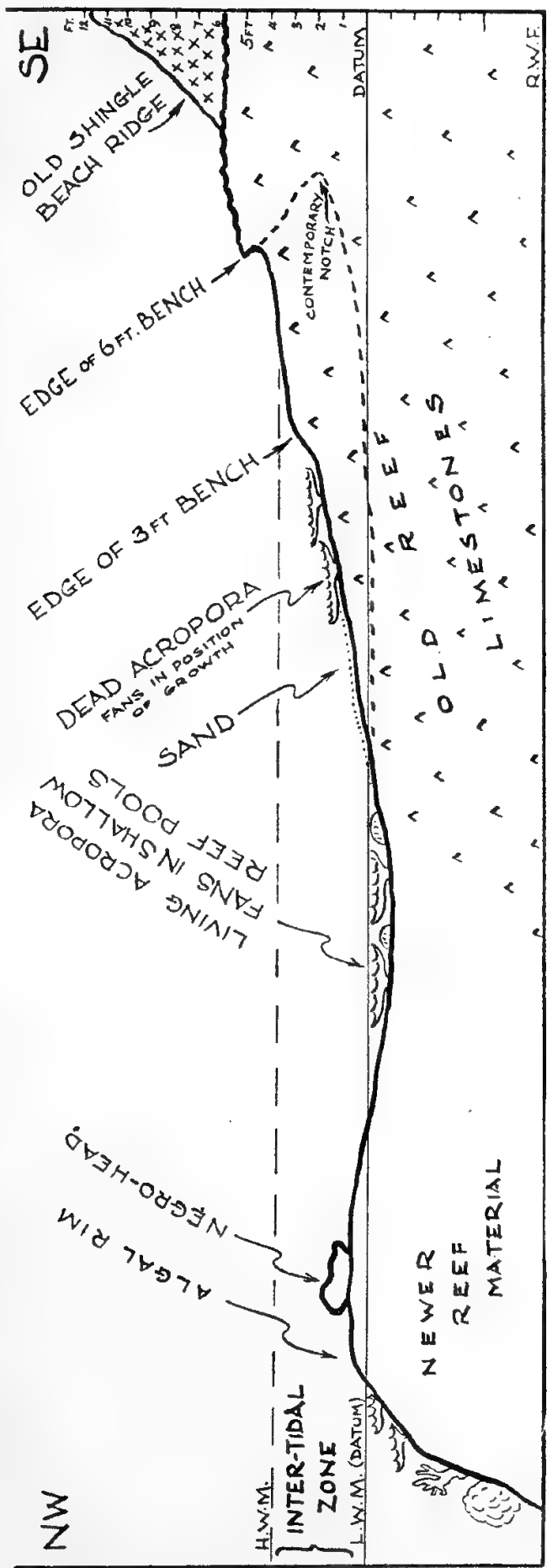
There is a small, circular pool or "pot-hole" 25 yards across in this platform near the western edge which fills at high tide by the sea filtering through the loosely cemented coral limestone. Even the inside cliffs bounding this pool are undercut (proving, if proof were needed, that the undercutting can have nothing to do with mechanical wave erosion). It is floored with a carpet of sticky white calcareous mud. A rather similar depression runs down the length of the islet, but is filled with mangrove (*Avicennia officinalis*). The same mangrove (which is fairly stunted in these islets, rising only to 20-25 feet) also occurs in small patches around the cliff-line, but is here and there overwhelmed by shingle invasions.

Over the surface of this platform are distributed series of ancient shingle beach ridges (mainly of flat, platy *Acropora* fans, together with short, stumpy lengths of branching types, just as described by Teichert (1947a, p. 154). In plan these ridges trend NE-SW, parallel to the exposed reef margin to the north-west, and their extremities curve away to the south-east. These old ridges rise to 12 and 13 feet. There is also a small (contemporary) sand-dune in the east part of the islet.

Contemporary shingle invasions lap up against and over the cliff-line in places in the north-west and west, to a height of about 6-7 feet. In certain places these newer beach ridges are themselves suffering wave erosion; this is particularly noticeable on the south-westerly, the most exposed of this little group of islets.

In places, a lower bench level may be observed in these coral limestone cliffs. This bench stands at about 3 feet above datum and is itself sometimes cliffed and undercut. From below this bench dead *Acropora* fans (of the very shallow-water type) in position of growth may be traced from about 1 foot 6 inches down to datum. The gradational aspect of this feature suggests that the latest drop in sea-level has not been a sudden one (see text fig. 3).





Text fig. 3.—Section, somewhat idealised, on the weather side of the Mangrove Islets. The basement consists of old reef limestone, probably with a veneer of newer reef material on the outer edge. Erosion benches have been left by the former sea levels at 5-6 feet and 2-3 feet. In many places, all trace of the 2-3 foot level is destroyed by the formation of a contemporary bench and undercut notch.

Almost all around Centre Islet and likewise around other members of the Mangrove Islets there are widespread patches of white calcareous mud on the reef-flat itself. There is generally no living coral within about 50 yards of the shore. From the severe undercutting of the cliffs and deep indentation of the shores it seems to be undeniable that these islets are in the process of very rapid destruction. That the erosion is by chemical solution in the sea-water is shown by the restriction of the effects to the intertidal zone and by its equal, if not greater, effectiveness in protected coves and bays. Since many of the smaller islets occur on continuous reef patches, we may well conclude that they have been isolated from each other by this means.

Thus, while there is vigorous coral growth in the outer parts of the reefs here, the inner sections, especially where the white calcareous mud has accumulated, most probably represent down-planed areas of former old coral limestone.

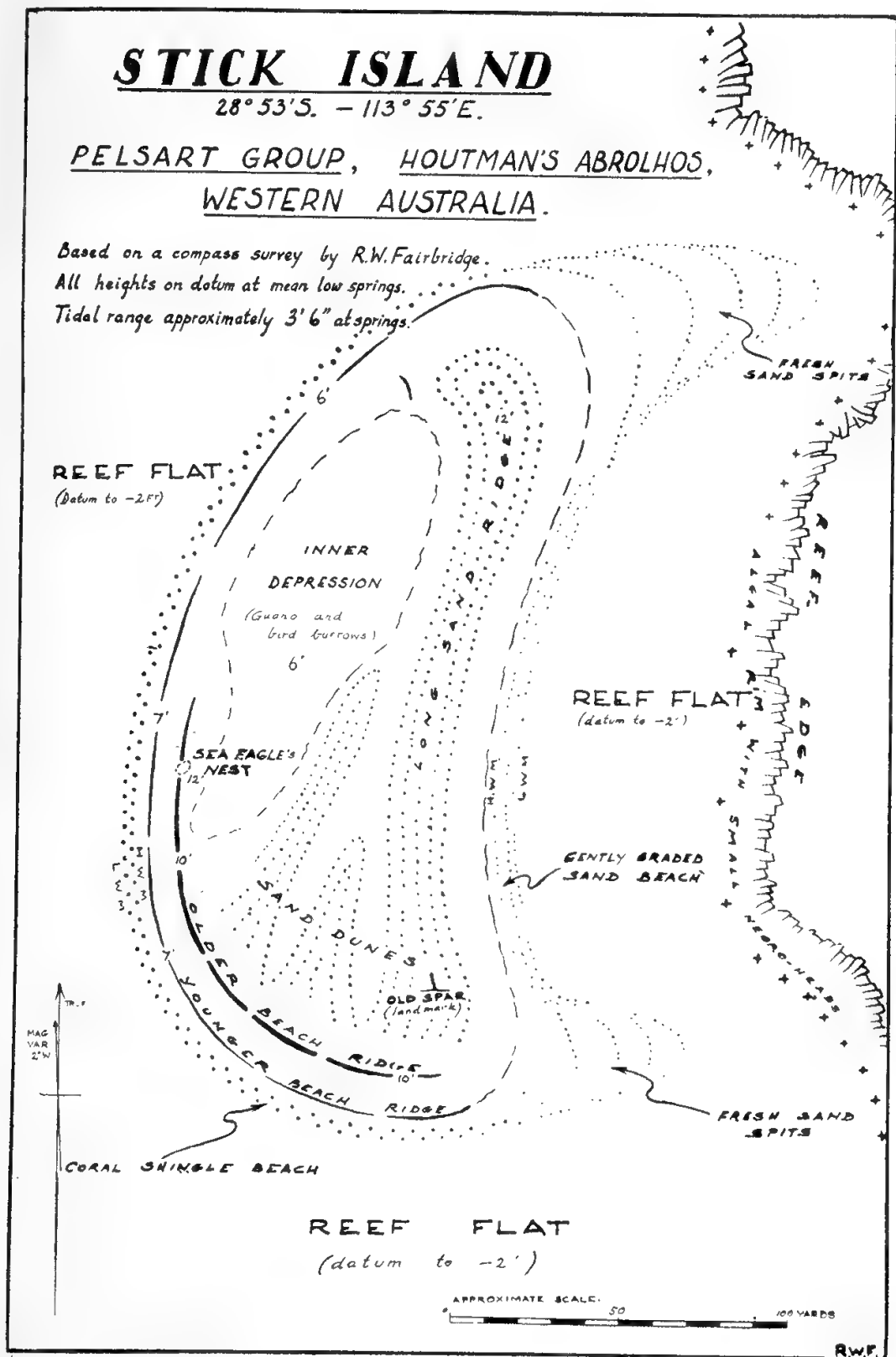
Clearly, the geological evidence in the Mangrove Islets suggests a somewhat variegated history. There is no direct evidence for ascertaining the age of the coral limestone, but by analogy with Teichert's work on Pelsart Island we might well place it in the late Pleistocene. There is, however, no obvious example of the 10-foot mid-Recent bench here and it may possibly be that this particular coral limestone in the Mangrove Group is younger than the Pleistocene coral limestone of Pelsart. In this case it could have formed during the mid-Recent 10-foot high stand and in any case became benched during the later 5-6 foot stand. (It may be remarked in passing that these two levels are so widespread in Western Australia, as well as overseas, as to be regarded as probably eustatic.)

The 5-6 foot bench next became partially covered by shingle beach ridges, as the sea gradually dropped to its next still-stand. (In Pelsart this would be Teichert's "low-level platform" and the beach ridges he estimates would have been forming since about 1000 A.D.) A further drop in sea-level somewhat later led to a localised benching at 2-3 feet above datum and after a short still-stand, the sea has slowly dropped to its present level. The advance of marine erosion in some places may perhaps suggest a slight rise during the last century.

The second type of islet reposing on the Northern Reefs is the shingle and sand cay type, of which we may take *Stick Island* ($28^{\circ} 53' \text{ S.}$, $113^{\circ} 55' \text{ E.}$) as a typical example.

The islet is 250 yards long and 100 yards across, rising to 12 feet above datum (see text fig. 4). It is sub-crescentic in plan, being orientated NNE-SSW, convex on the north-west, the weather side, and concave to the lee. Its perfect smoothness in outline is in striking contrast to the excessively jagged outline of the Mangrove-type islets. It has no cliffs at all and only a stunted vegetation, without mangroves.

The whole of the convex perimeter consists of a steep shingle beach rising up from the sediment-strewn reef, which grades down to about 2 feet below datum level, with extensive living coral at its fringes. The shingle beach rises up into a steep-sided beach ridge 7 feet above datum



Text fig. 4. Sketch-Map of Stick Island.

and 10 yards behind it there is an older beach ridge rising to 10 feet.

The concave side of the islet, on the other hand, is a gently sloping sand beach. On the day I visited the islet, just after a westerly gale, the two horns or spits at either tip of the crescent were both considerably elongated by accumulations of fresh sand.

Within the higher shingle beach ridge, in the south-west, there are series of low sand dunes, which may in part be old sand beach ridges. In places they rise to 12 feet. Only the outermost of these continues right up to the north-east corner, however, and in behind the shingle beach ridge in the north-west, there is a shallow depression, at about 6 feet above datum, which is floored with sandy guano with some coral boulders, and honeycombed with bird burrows.

The history of this type of islet must certainly have been fairly short. There is no definite coral which has grown in place. The older beach-ridge, however, at 10 feet above datum appears to be well beyond the capacity of present-day wave building. It may be correlated quite closely with similar ridges formed during the 5-6 foot sea-level in the Mangrove Group and Pelsart, which Teichert has regarded as dating from 1000 A.D. The seven-foot beach ridge may, for its part, be partly formed during the 2-3 foot stand and at the same time be partly contemporaneous.

(c) THE CENTRAL PLATFORM REEF, ITS ISLETS AND THE LAGOON.

At high tide, the interior of the Pelsart Group appears to be nothing but a wide lagoon, surrounded on all sides by reefs and islands, and dotted by a few scattered islets within. Observations at low tide, soundings and aerial data, however, show the position to be more complicated.

To the interior of the south-western reef, there is a broad platform, extending from end to end of that reef and inwards towards the centre of the lagoon. This platform lies mostly at about low tide level, but actually varies from 1 to 2 fathoms in depth rising in isolated islands up to 12-18 feet above datum. It is not composed of living coral, but mainly of a hard white compact limestone. This rock contains fossil corals of apparently slightly deeper-water character, including some varieties of *Favites* up to 4 feet in diameter. Delicate *Acropora* fans and branching types are notable for their absence in it. Certain pelecypod shells, such as *Katelsia*, are common. Its general appearance is one of relatively great antiquity. Extending northwards, this platform reappears as a smooth rock shelf, eroded down to about 3 fathoms, to form the basement of the westerly of the northern reefs and islets. There are some deeper channels in it, but most of this area is of fairly constant depth and consists of a smooth limestone floor with a thin layer (in places about 1 foot thick) of white calcareous sand or mud.

To the east, along the inner side of Pelsart Island, there is a similar, though narrower, shallow limestone platform and there may also be some evidence for a submerged, 3-fathom platform. In the northern part, however, around the margins of the existing platforms and rising up from the floor, there are contemporary corals growing in profusion in a zone about 6 miles long and 2 miles across. This is Dakin's

so-called "Maze" (Dakin, 1919). From the aerial photographs (see Plate III) it may be seen that this area consists mainly of an ordinary rock platform eroded into a honeycomb pattern, enclosing round "sink-holes," pot-holes, occupied by pools of fairly deep water. Dakin has already noted how many of these pools drop straight down to 15-16 fathoms. Their margins are lined by particularly luxuriant coral growth, which gave Dakin the impression that they were exclusively coral, whereas there almost always seems to be a basic skeleton of older, eroded limestone. (A suggested explanation for this phenomenon will be discussed under the heading of "(g)—Reef Erosion.")

The same massive white limestone is also found rising to a height of 18 feet on East Wallaby Island (see Teichert, 1947a, p. 173), so here is a core of the same material as the Central Platform.

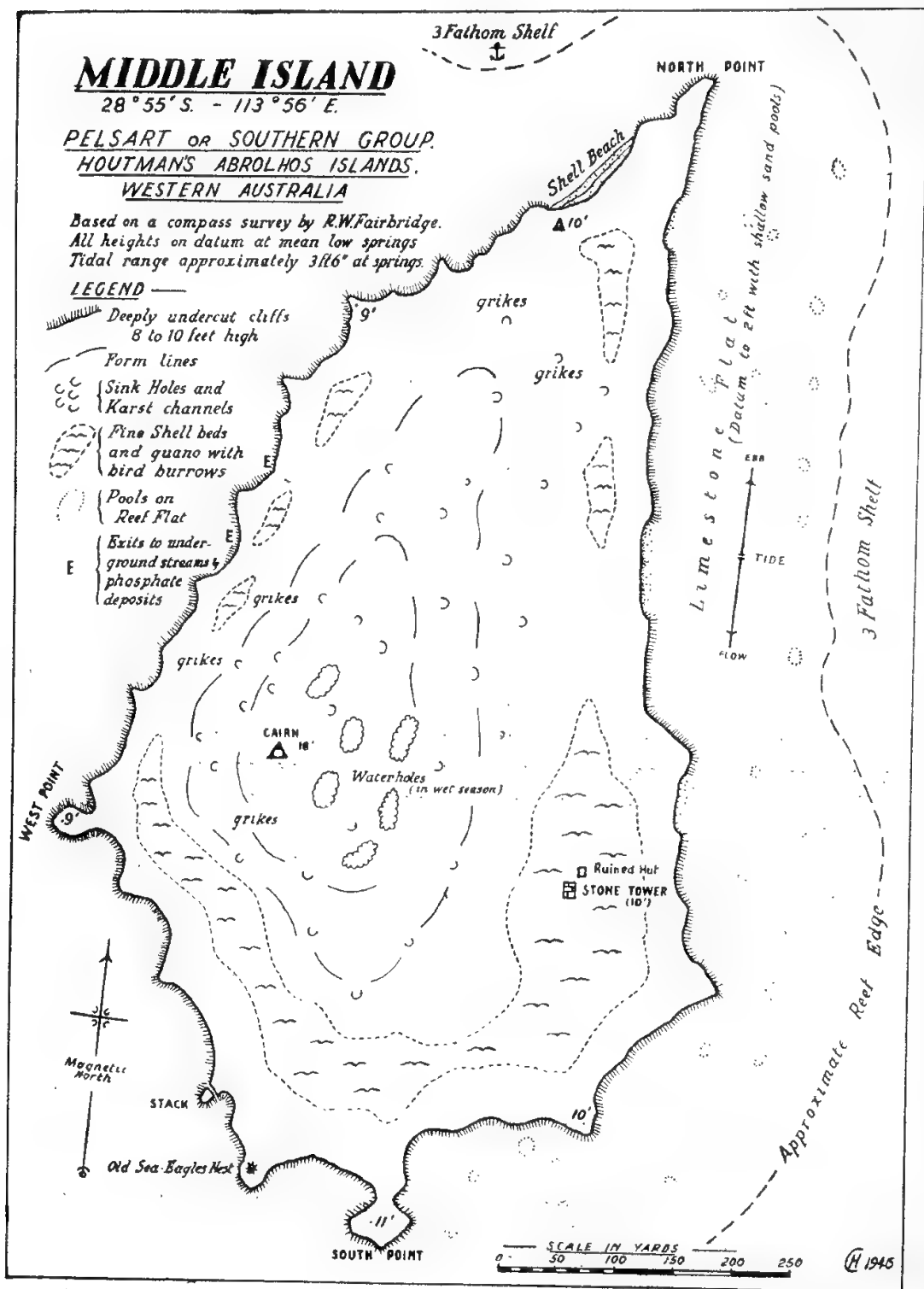
The western side of the Pelsart Platform is separated from the eastern side of the Central Platform by a broad channel of 10-15 fathoms depth, which runs in a north-south direction from Wreck Point northwards, so as to practically bisect the entire platform of the Pelsart Group. This Middle Channel is the usual ship entrance to the lagoon and forms a direct and well-protected passage right down to the former phosphate loading jetties at the south end of Pelsart Island.

As noted already, the surface of the main platform lies mainly at about low-water level, but in places descends to one or two fathoms depth. It is a remarkably smooth plane of erosion and the truncated tops of fossils incorporated in the limestone can often be observed on its surface. The complete absence of living coral over the south-western part is also quite striking. Very small tufts of green weed and algæ adhere to it in places; in others, there are large colonies of serpulids or *Vermetus*. Circular pools a few inches to a foot in depth dot this surface and these are partly filled with sand, weed and microscopic life. In deeper sections, long narrow sand-pits extend out on to it from the edge of the outer reef in the south-west. It is understandable from the ecological point of view that such an area would only support a limited and extremely tolerant type of life, since water temperature variations alone, on such a flat, would vary at times through a range of over 40° F.

Teichert has described a very similar platform between the East and West Wallaby Islands, except that he says it consists of dead coral reef limestone. It is covered with green algæ, "but otherwise there is surprisingly little life on it."

The islets which rise up from the Central Platform are remarkable in many ways. They differ not only from the complex accumulation of Pelsart Island, but also fundamentally from the coral limestone islets of the Mangrove Group, and equally again from the sandy cays of the Stick Island type. They include Middle Island, Gun Island, Green Island, and the cluster of smaller islets 2-3 miles west of Middle Island (numbered "One" to "Eight").

Middle Island is the largest of these islands and we may take it as the type example. It lies at 28° 55' S., 113° 56' E., and as the name



Text fig. 5. Sketch-Map of Middle Island.

implies, just about in the centre of the Pelsart lagoon, marking the western edge of the Middle Channel.

The island is almost exactly 1,000 yards long in a north-south direction and 550 yards across (see text fig. 5). Its highest point is 18 feet above datum. In the south-east there are some ruined stone buildings, including a stone tower 10 feet high (the top is thus 20 feet above datum) from which a commanding view may be had of the whole lagoon, no part of its rim being more than 6 nautical miles distant.

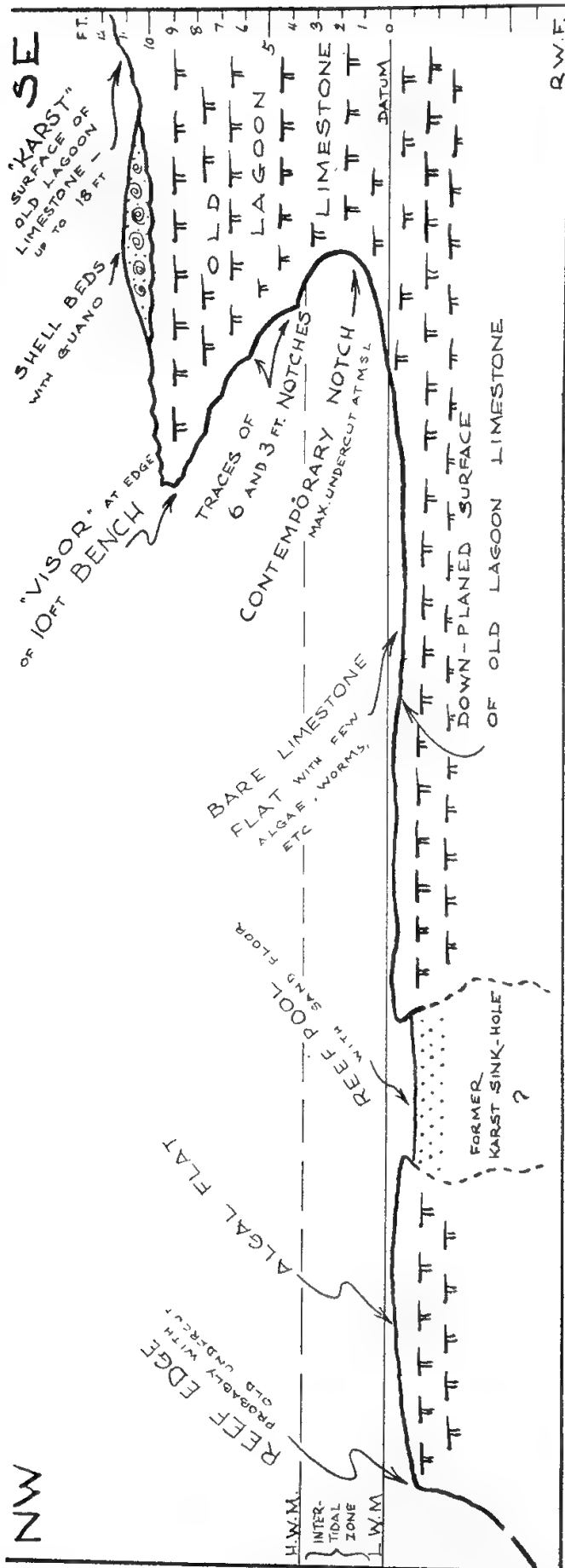
Middle Island is entirely surrounded by an overhanging cliff, 8-10 feet above datum. It is deeply undercut by the solvent action of sea-water, the notch reaching in from 6 to 10 feet in places and forming small caves. In places the visor, or overhanging part, has collapsed. The situation is very much like that described on West Wallaby Island by Teichert (1947a, p. 175). Wave erosion is utterly discounted since the entire island is surrounded by a wide datum-level platform, which protects the cliffs, except for small wavelets at high tide. The maximum undercut is about mean sea-level, where the rock surface is etched and pitted in the usual way.

The perfect undercut today, found in the more exposed places, is a somewhat jagged parabolic curve from the lower lip of the visor. From a distance this curve often looks remarkably perfect, but closer examination will reveal its heavily etched surface.

In less exposed sections, however, we sometimes find irregularities in this curve, which in rare places are disclosed as relics of older and higher notches. In exceptional places these may be followed up in steps. Intermediate notches of this sort may be correlated with sea-levels 2-3 feet and 5-6 feet above the present. The centre of the notch will of course be somewhat higher, in order to allow for the additional height of the then-existing mean sea-level (see text fig. 6). The heights of the older notches will thus come at above 4-5 feet and 7-8 feet above datum today. Since the 4-5 foot level corresponds very closely with the present low-limit of blackening on the surface of the old limestone, this becomes a particularly striking feature. The older, higher, and even less perfectly preserved level at 7-8 feet is without this special contrast and is relatively less obvious (see Plate II).

At the foot of the present notch, in places the surface of the platform is polished smooth. It was observed that the ebb tide performed a considerable scouring action here, with small shells and calcareous sand as the abrasives. On both the western and eastern sides there are several small beaches consisting exclusively of minute shells, mostly gastropods of the *Coxiella* type.

Above the cliffs is a broad platform of about 10 foot altitude. The margins for 5-10 yards from the cliff are bare and deeply eroded, but then to the interior is a belt, 10-100 yards in width, of shell beds, mostly riddled with the burrows of sea-birds and liberally mixed with guano. These shells are of a remarkably constant size, about one-quarter to one-half inch in length, and of very few species of gastropod and



Text, fig. 6.—Section through the reef off Middle Island. Horizontal scale greatly reduced. The basement consists of old lagoon limestone (late Pleistocene). In a few places there is a little living coral on the reef edge. The outer part of the reef is mostly covered by algae, though not generally of the coralline type, while the inner part is largely a bare surface of the old limestone, showing truncated fossils of corals, pelecypoda etc. The reef flat is interrupted by shallow pools here and there, which may be former "karst" sinkholes. The 10 foot benched cliffs with old shell beds are relics of a mid-Recent high sea-level (10 feet above the present datum), while the undercut is notched here and there by traces of the 5-6 foot and 2-3 foot late Recent sea-levels.

pelecypod; a few small coral pebbles are included. Low scrub marks this zone.

These beds grade irregularly from almost pure coquina (unconsolidated) into grey sandy shell beds and then into a low-grade guano. Teichert appears to have observed similar shell beds on Pelsart Island, also overlying a fine-grained massive limestone and in a similar relationship to the guano. They certainly correspond exactly with his terrace of old beach deposits at $6\frac{1}{2}$ feet above high-water level (*i.e.*, $6\frac{1}{2}$ feet plus $3\frac{1}{2}$ feet (to datum) making 10 feet, their observed level on Middle Island). Teichert recorded similar terraces corresponding to $8\frac{1}{2}$ and $6\frac{1}{2}$ feet above datum, and "raised" beaches of this height occur near the northern point of Middle Island. Teichert has noted that these shell species do not occur on the lagoonal flats today, and according to his estimates would appear to date from the very recent periods of higher sea-level.

Rising gently inland appears the bare limestone, with but the merest patches of soil, to form a low rise, asymmetrically placed on the west side of the island. Jointing has broken the limestone up into large, sharp-edged slabs. Its surface weathers light grey and is etched by solution channels, grikes and deep pot-holes up to 3 feet in diameter. Underground channels have collapsed in places to form small-scale karst "dolinas" up to 6 feet deep. The floors of these depressions are filled with soil. In some of the smaller ones, water collects in the wet season, and in others, tomatoes have been planted by earlier visitors, and though the fruit is small, they still make good eating.

The limestone rock-material of this Central Platform Reef and its islands has also been found by Teichert on the southern part of Pelsart Island and in the Wallaby Group, where rather similar karst features were noticed. He has called it the "Shell Limestone," to distinguish it from the essential coralline nature of the other limestones there. It is a fine-grained, fairly massive limestone, which he describes as resting on the top and in pockets in the earlier reef limestone that forms the basement of these islands. Teichert attributes it to deposition during the latter half of the Mindel-Riss inter-glacial, suggesting that a probable sudden rise of sea-level extinguished normal reef growth. (Further discussion of this correlation will be found in Section III.)

My own impression is also that there was certainly some such rise in sea-level, and that these limestones are normal lagoonal deposits. The white fine-grained matrix of nearly 99% CaCO_3 is typical of the white amorphous calcareous mud which is being laid down around the lagoon today. We might, therefore, describe it more vividly as a "Lagoon Limestone."

It is notable that Teichert only found it amounting to about 3 feet in thickness, resting on a basement of coral limestone on Pelsart Island. Even here he observed: "It has the features of a lagoon deposit, but its fauna is unlike that of the lagoon shore of the present day" (*loc. cit.*, p. 162). On East Wallaby Island this shell or lagoon limestone is reported to be 6 to 8 feet thick and rests on the reef limestone at only

2 feet above high-water level. In this locality he also noticed the similarity between it and the contemporary sediments on the southern side of that island. In Middle Island, on the other hand, this limestone is measured over 18 feet in thickness and its base was not sighted. I had the impression from the nature of the karst solution, that it went down to considerable depths. This would all fit in with concept of a lagoon limestone, more or less contemporaneous in origin to the coral limestone that formed around the periphery of the group.

So much for Middle Island, and it appears to be more than likely that a similar description would fit Green Island, Gun Island, and the eight others rising from the western part of the Central Platform. It was unfortunately impossible to visit all of them, but from observation, they all appeared to have precisely the same undercut cliffs and flat limestone platforms rising from about 10 feet to 15 or more feet in the centre.

Attempting now to find an explanation to fit these curious islands, it is at once clear that they are erosion relics. In fact, there is a very small one, flat-topped, with undercut cliffs, less than 100 yards across, lying over a mile south of Middle Island. We may say that they all appear to be remnants of a once broad platform of Pleistocene lagoon limestone which extended over the whole triangle of the Pelsart Group, ranging from 18 feet above datum down to an unknown depth below. On the margins it overlaps, or interfingers, but thins rapidly over a broad rim of slightly older coral reef limestone. It may be correlated with a period of high sea-level, at least 18 feet above the present.

This platform must have been severely dissected during the succeeding glacial periods of lowered sea-level and a great part of the central platform was eroded away by a network of small streams and by one main central stream which drained the area towards the north. It is probable that during the last glacial this land was in the form of a basin-like plateau on a peninsula, about 250 feet above the sea-level then, connected to the mainland by a neck of lower country in the east. The south-east and south-western sides would have been precipitous, while drainage to the north would have reduced the topography there to a series of broad valleys.

Finally, it appears from the preliminary evidence of a series of soundings on the floor of the lagoon, which are as yet insufficiently complete as to be decisive evidence, that there were intermediate periods of still-stand in these subsequently rising sea-levels at about 3 to 15 fathoms.

(f) REEF GROWTH.

Corals are growing today, in all probability, in a continuous belt around the outer perimeter of the atoll. However, as soon as each individual colony reaches into the realm of violent wave action, it is broken off and thrown up on to the edge of the established reef and there consolidated by the activity of calcareous algæ, such as *Lithothamnium*. This appears to be a slow but relentless process, which does not fundamentally alter the outer shape of the atoll, but operates continuously in an outwards direction.

To the interior of the group, in the lagoon, however, we have observed that there are two fundamentally different types of reef. The one is "dead," an eroded limestone, while the other is living. It is with the latter that we shall deal with here. Only in the vicinity of the Mangrove Islets and the north-east part of the lagoon are there large patches of coral actually at the surface.

It appears that in many parts of the lagoon, live coral is growing up from the floor in 3-15 fathoms. Where this growth is initiated in independent spots, the corals tend to grow up in pinnacles or "coral-heads." On reaching the surface the coral growth is directed outwards to give the whole thing a mushroom shape. When this overhang becomes excessive, bits of it drop off and these help to strengthen and fill up the base.

This growth of pinnacles, or coral-heads, develops to a point where the different patches begin to unite and gradually a complete network is formed. However, by this process there are always gaps left behind and these tend to be reduced gradually to more or less narrow channels, in which coral growth is more restricted than out in the open lagoon.

In areas of active growth, such as in the Mangrove Islets, one may detect a gradual transition from the actual dry land to the massive "fringing reef," to the open network of reefs, to the large, separate coral heads and patches finally to scattered heads which do not yet even reach the surface.

Even on the apparently massive reefs not far from the shore, there can often be observed a series of narrow channels, a few inches wide near the surface or even bridged right over, which appear to widen out underneath. These appear to be "sutures" where the radiating growths from different coral patches have finally met. I have seen large segments of these overhanging coral patches which have broken off from their slender stalks and now lie tilted over at an angle of 20° or so. Coral growth is fairly meagre in these "underground" channels, through restriction of light, food supplies, etc., and it must be a matter of some time before sediments and organic debris actually fill them up. In general, these appear to be examples of what were described from Bikini Atoll as "room-and-pillar" structures by Tracey, Ladd and Hoffmeister (1946).

On the surface of the reef there are shallow depressions only a foot or a few feet deep; in these there is generally a fairly scattered growth of corals. The heads of the *Acropora* fans especially, when killed by exposure, generally bleach and soon become attached with little tassels of algæ growth. Gradually miscellaneous sediments and calcareous muds block up the whole surface of the reef so that coral growth is virtually excluded from it.

On the margins of each reef patch or platform in the lagoon there is a raised rim of debris cemented to the reef and smoothed over by calcareous algæ (see Plate I, figs. 1 and 2). This rim varies, according to the exposure, from a few inches to about 2 feet above datum, and appears to form by the heaping up of debris broken off from the grow-

ing corals of the reef edge under the influence of waves, even though in the protected lagoonal area the latter are never large. The process seems to be a perfect miniature reproduction of what goes on at the outer oceanic edge of the main reefs, where the true *Lithothamnium* Ridge is formed.

Thus by coral growth, cementing by the deposition of calcareous muds and breccia, and veneering by coralline algæ, the reef is built up, solidified and strengthened. On the shore, beach ridges will accumulate and will tend to build up the land. There can be no doubt that the serried ranks of beach ridges all around and over the surfaces of many of the islands, serve well as a protective blanket against the forces of erosion. And especially around the outer perimeters where marine solution is highly active, fresh layers of coral shingle must go far to make up for, if not totally counteract, the forces of solution.

It is true that at many points we observed, as Teichert has already (1947a, p. 193), how shingle material is being washed away, a feature which suggests a slight contemporary *rise* in the sea-level (for further discussion of this subject, see Section III).

But on the whole, however, the forces of erosion, even with the sea in a state of still-stand, would appear to be greater than those of accumulation. Only by repeated eustatic oscillation is the reviving breath of fresh coral growth re-introduced to provide material for island-building.

(g) REEF EROSION.

As equally as corals and associated living organisms are growing, and mechanical and chemical processes are adding bulk to the reef as a whole, a contrary set of processes are tending towards the destruction of the reef. The latter fall into three main groups:—

- (i) Biological.
- (ii) Mechanical.
- (iii) Chemical.

An important feature of all destructive processes, however, is this: their sphere of action is mainly concentrated in the intertidal belt. Certain subaerial processes will cause the decay of old coralline material above high-tide line and certain biological attack will continue a few feet below the low-tide line, while mechanical erosion by wave action is experienced down for several fathoms, but at greater depth there is no evidence of any destructive process. (It will be remembered that Sir John Murray and his followers believed that chemical solution by sea-water was the explanation of lagoons. Of such a process, there is no evidence below the inter-tidal zone.)

(i) *Biological Erosive Factors.*

In all the reefs, whether of living coral, coralline algæ or limestone, there is extensive boring, burrowing and dissolving action by various types of animal and plant. Polychaete worms play a major part; then there are the boring pelecypoda, the nibbling action of certain gastropoda, echinoids and of certain fish. It appears that certain

gastropoda (e.g., *Patella*, *Haliotis*) probably by some chemical action, hollow out pockets with their sucker-feet. Mayor (1924) has already demonstrated how holothuria devour enormous quantities of coral sand and reduce it to still finer particles, as well as bringing about its solution.

None of these factors by itself may seem to be of great significance, but together they combine to so loosen and expose the outer six to twelve inches or so of reef, so that the far superior forces of mechanical and chemical erosion, to be analysed below, can carry out their attacks with greater effectiveness.

The activities of these biological factors in the Abrolhos seem to be mainly restricted to the living reefs, that is to say, those of recent coralline material. The reefs of more resistant lagoon limestone appear to be remarkably poor in organic life, and on their down-planed surfaces there is relatively little evidence of biological erosion. There is some, however, as shown by occasional patches of green algæ, and by odd colonies of *Vermetus* and *Polydora*-like worms, just as described by Teichert on East Wallaby Island (1947a, p. 173).

(ii) *Mechanical Erosive Factors.*

On the outer edges of the reefs the relatively delicate, living coral structures are exposed to the full force of breaking waves. The effect of the latter is felt, of course, well below the low-tide limit, for several fathoms. In this way fragments of the deeper water corals are thrown up on to the reef surface. A rim of such debris tends to accumulate on the outer edge of the reef, while ridges of similar debris develop around the beach-lines.

On the reef-flat itself the larger debris is steadily reduced to the dimensions of sand, and the wave swash and tidal currents transform the sand in suspension into a further, very powerful erosive scouring agent. The effect of this scour is to smooth and polish the reef rock material on the reef flat, but above mean sea-level the polishing becomes less and less apparent until by the high-tide limit no trace of it remains.

In the Pelsart Group major mechanical erosion is more or less restricted to the outer margins of the peripheral reefs, and it is only here that sand and shingle accumulations form. On the margins of the inner reefs, where the width of the lagoon permits a moderate "fetch," there is a very reduced amount of fragmentation of growing coral by wave action. Minor scouring, however, is evident over many parts of the Central Platform, where the currents set up by the rising and falling tide are an important factor.

(iii) *Chemical Erosive Factors.*

The third erosive factors are the chemical solvents, rain water and sea water. Rain water is normally a fairly acid medium which will cause extensive solution in all coral material and limestones above sea-level. Percolation of such water through these previous accumulations will continue down to base-level (which varies slightly with each tide). Solution effects are therefore produced, leading to "karst" phenomena, as noted on Middle Island and elsewhere.

Sea-water, on the other hand, is normally alkaline and represents a buffer to such solution, inhibiting further rain-water solution at the level of the prevailing tide. Nevertheless, the fact remains that there is extensive evidence of severe chemical solution within the inter-tidal limits, and of a type which is considerably more rapid even than that caused by rain-water.

These solution effects extend from low-tide level up to the limit of wave splash above high-tide, but reach a maximum almost at mean sea-level on protected shores, reaching somewhat higher at exposed points. Above mean sea-level the coral limestone is etched and pitted by the solvent to make a very jagged surface indeed. But below mean sea-level this roughness tends to be evened down by mechanical abrasion and in places where there is sand it is quite effaced by polishing.

There is no sign of solution more than an inch or two below low spring tide level. On cliffed shores there is very deep undercutting at about mean sea-level, which in places extends 10 to 15 feet under the cliff. Where the cliff itself is only 10 feet high, as is often the case, a very striking "visor" effect results.

Hitherto there has appeared no adequate explanation for the production of these solution phenomena by sea-water, though their existence has been specifically recorded in the Red Sea by Macfadyen (1930), in the East Indies by Kuenen (1933), in the Pacific by Stearns (1941, etc.), in the Great Barrier Reef by Fairbridge and Teichert (1947), and already in the Wallaby Group of the Abrolhos by Teichert (1947a). From personal observations, from a study of the literature, and from both ground and air photographs of a great number of Pacific coral islands examined during the Japanese War, I have concluded that these solution effects are almost universal along coasts of calcium carbonate material.

As is well known, sea-water, with a pH over 8 is normally alkaline in its effect. And in warm latitudes it is generally supersaturated in calcium carbonate (see, for example, Harvey, 1945). Theoretically, one may conclude that it is impossible for it to take more carbonate material into solution. While it is realised that in the complex chemistry of sea-water there are a great number of associated factors bearing on the subject of calcium carbonate solution, the following tentative explanation is put forward in simplified form. It has two aspects, probably complimentary, physio-chemical and biochemical, and we shall deal with the physio-chemical one first.

On the wide reef-flats, and especially at low tide, a considerable rise of water temperature has been recorded on warm sunny days. Records by Mayer at Murray Island at the northern end of the Great Barrier Reef (1918) have been paralleled by similar readings in the Abrolhos. A normal sea temperature of 19°C. will rise to 27°C. in a few hours on the reef-flat. Now, a rise in temperature causes a reduction in CO₂ solubility, and a rise in the pH. Calcium carbonate then come out of solution, being precipitated as a fine white powder. Similar observations have been made on Great Bahama Bank (Black, 1933), in the Indian Ocean reefs by Gardiner (1930), and elsewhere. Bacteria

take some part in this action, but it is not quite clear how much (Bavendamm, 1932). Large deposits of this amorphous white mud are found in all protected parts of the reef-flats (as also by Teichert on the Wallaby flat, 1947a, p. 173). Even in the deeper waters of the lagoon we noticed how the otherwise crystal-clear water suddenly went opaque and milky at a certain stage in the ebb tide. It appears as if with the outgoing tide suspended calcium carbonate is carried off the reef-flats and deposited on the floor of the lagoon, some even being carried out to sea.

It is now suggested that in the evening a reverse process will take place. A great reduction in temperature has been recorded in the shallows after a cold night. Under such conditions, more CO_2 is taken into solution and the pH drops sharply. From being formerly super-saturated, the water is now under-saturated and is more like an acid in respect to calcium carbonate. Solution will now take place on the clean surfaces of coral limestone exposed in the upper part of the reef-flat and undercut cliffs.

Careful temperature measurements show that only the shallow surface layers of water on the reef-flats are affected by these extreme variations in temperature. At various times on the reef-flats I have measured temperatures ranging from 27°C . down to 14°C . Beyond the edge of the reef, on the other hand, the water temperature does not change more than 1°C . or 2°C . for weeks on end. So it is only a thin layer of water nearest the shore which is endowed with this solvent property.

On *a priori* grounds one might conclude that with tidal fluctuation it would be at mean sea-level where the maximum solution effects would be found. And it is precisely at this level that the cliffs are found to be furthest undercut. Kuenen (1933), as a matter of fact, has spoken of the "sawing" effect of the sea on the limestone cliffs at this level.

An additional factor which appears to work towards the same end as the above-outlined, purely physico-chemical one, is a biochemical one. Additional CO_2 will be liberated by reef animals at night, while during daylight this source will be more than used up by the reef plants in their photo-synthetic reactions. Revelle (1934) was even of the opinion that this was the most important factor in controlling CaCO_3 solubility.

In order to explain the little solution basins commonly found on most coastal limestone reefs and benches, Emery (1946) has carried out extensive tests, and has certainly shown how the pH variation (and resultant solution) is largely controlled by the CO_2 from marine algæ. While this biological factor is certainly recognised in the major problem of reef erosion, I do not consider it to be the only one—at least, in the light of my observations to date. In particular, there is no reduction in the solution effects on the cliffs of, say, Middle Island, which is one of those surrounded by wide flats of old lagoon limestone, in contrast to the cliffs around the Mangrove Islets, which are surrounded by living reefs. The old lagoon limestone flats of the Central Platform are

astonishingly devoid of life, algal or otherwise, and one may walk upon the smooth-polished limestone surface for hundreds of yards without finding more than a few hardy species. On the living reef-flats, however, there is teeming life, plant and animal, of every variety. Yet the etched and eroded limestone cliffs behind each are much the same.

An economic aspect of this contrast between the old limestone reefs and the contemporary living reefs is the way in which the Abrolhos cray-fish (*Panulirus longipes*) are almost exclusively inhabiting the live reef margins. The difference between the two types of reef, recognisable on air photographs, should have economic significance for fisheries development.

An interesting feature of the reef-flats which have been cut down out of old lagoon and coral limestone, is the occurrence of rounded "sink-holes" or "pot-holes" of large and small dimensions. They range from 1 or 2 feet across to as much as 100 yards or more across. It seems that they may either be filled with fine sediment and coarser debris, reducing them to a few feet, or even inches in depth, or they may be of considerable depth, going down many fathoms. Their margins tend to be etched out by chemical action, but the deeper ones may have a fringe of contemporary, growing coral around the lip.

From a careful study of these features on the ground and from the air photographs in the vicinity of Pelsart Island it is believed that these pot-holes cannot be of contemporary formation. Their shape, even when fringed with live coral, suggests chemical solution, from the interior of a pre-existing rock working outwards, and not the "cauliflower" pattern of living coral, which, of course, grows by accretion on to the exterior of the pre-existing reef, or upwards from the lagoon floor.

The following explanation is suggested: deep dissection of the Pleistocene-formed lagoonal and coral limestones during the last glaciation (Würm) with its low sea-level would have caused an extensive system of subaerial solution channels, caves and pot-holes to develop. With the succeeding Flandrian transgression this old karst landscape would have been drowned, permitting coral colonisation on all the old surfaces now submerged. The subsequent drop in sea-level of ten feet has led to the planation of old irregularities down to the present low tide-level, while coral now grows in profusion around the peripheries of the old karst pot-holes and depressions.

III. CORRELATION AND EVOLUTION.

As will appear by comparing Teichert's results on Pelsart and Wallaby Islands, and also at Rottnest Island, 250 miles to the south, and as I have been able to confirm at numerous points along the coast, such as Dongara, Jurien Bay, Moore River, Scarborough, Cottesloe, Point Peron and Garden Island, there is a uniformity in West Australian coastal physiographic features that demands eustatic rather than local explanation.

We now recognise, with some fair degree of confidence, three for-

merly higher sea-levels, at 10-11 feet, 5-6 feet and 2-3 feet above the present datum (low springs) which are expressed by means of eroded rock benches, undercut notches, former beach deposits and shell beds, etc.

Periods of still-stand of formerly lower sea-levels are also suggested by certain uniformities in bathymetric soundings; owing to unreliable data, and the absence of sonic sounding material in these waters, we are less sure of these figures, but 55 fathoms, 40 fathoms, 15 fathoms and 3 fathoms seem to be the particularly significant levels.

All these levels are found in, or in the vicinity of the Pelsart Group of the Abrolhos, and in addition, the formation of lagoon limestones and old coral limestones to heights over 18 feet suggests evidence for an even higher sea-level at one time, perhaps of the order of 20-25 feet above the present datum.

It might appear at first sight dangerous to attempt a long-range correlation of this material on absolute sea-level measurements alone, but the coincidence between these levels and others, measured in similar stable areas of the world, is so striking that in recent years geologists have gained some confidence in this direction. They are not identical, of course. One would not expect it so, since even the present sea-level is not everywhere geodetically constant. Unfortunately, many earlier attempts have been based on insufficient evidence, inaccurate levelling, ignorance of tidal characteristics, of exposure and erosional characteristics of the rock materials. Others again have been attempted in regions of patent crustal instability, an obviously dangerous proceeding.

I believe it is possible, therefore, to correlate these West Australian levels with those of other stable areas, and for sake of interest, I shall give an absolute dating of these Quaternary levels, suggested by Zeuner in his latest works (1945, 1946). While the subject of absolute dating is still a somewhat contested one, there now appears to be a sufficient convergence of evidence, achieved via many routes, as ably summarised by Zeuner, to make it at least interesting to correlate these dates with our sequence.

It must be pointed out, as by Teichert already, that no palæontological work whatever has been devoted to the Abrolhos Quaternary material, and so from that aspect we are completely in the dark. The field, however, is a most promising one.

Thus bearing our many limitations in mind, a review of Quaternary events in the Abrolhos may read as follows.

As is well known amongst students of the Pleistocene, the interglacial warm periods were marked by world-wide rises in sea-level. Following Zeuner (1945, p. 252), towards the end of the last (*i.e.*, Riss-Würm) interglacial, that is, about 125,000 years ago, the world sea-level stood 7.5 m. (25 ft.) higher than it is today, forming what are known in the Mediterranean as the Late Monastirian terraces. This would be an adequate level for the formation of our old lagoon and coral limestones in the Abrolhos. Teichert (1947a) had actually com-

pleted his MS. *before* the publication of Zeuner's book and had at that time suggested that these limestones be correlated with the earlier, Mindel-Riss interglacial, as it was one of the longest and warmest of those periods. However, the sea-level associated with this interglacial was considerably higher (forming the 100-foot Tyrrhenian terrace in Southern Europe). While, of course, it is quite possible that our oldest limestones in the Abrolhos were formed during one of the earlier interglacials, it would be necessary to assume that a very considerable thickness had been entirely eroded away by today. Furthermore, as Teichert notes (*op. cit.*, footnote to p. 187), there is this close agreement between the Late Monastirian levels and the top of the Abrolhos limestones.

With the ensuing drop in sea-level, corresponding to the Würm glaciation, the whole of the continental shelf and the Abrolhos became dry land. There appears to have been a world-wide still-stand of sea-level at about 55 fathoms (100 m.), and there is certainly evidence for a notable change in slope at or about 55 fathoms at many points along our coast. This, according to Zeuner, would have been about 115,000 years ago. As the sea rose again, probably in a series of oscillations, there appear to have been periods of still-stand at about 40 fathoms (70 m.) some 72,000 years ago, and at 15-16 fathoms (30 m.) 23,000 years ago, before the completion of the Pleistocene epoch at about 7,000 to 8,000 B.C. (*Yoldia* time), after which it rose with the so-called Flandrian transgression to more or less the present-day level by about 4,000 or 5,000 B.C.

In the regions of Northern Europe at this time occurred the transgression of the *Litorina* Sea, but Zeuner (1946, p. 104) points out that its movements were so largely conditioned by isostatic reactions there that, as a chronological or horizon marker, it is unreliable. Teichert (1947, p. 188) believes that an 18-foot sea-level corresponding with it can be recognised in the form of negro-heads above this level on East Wallaby Island, but, for myself, I was unable to find any evidence of a eustatic level of this order in the islets of the Pelsart lagoon.

In Europe there is evidence of a somewhat constant low stand of the sea at about 3-4 fathoms between 2,000 and 4,000 B.C., which is certainly interesting in view of our Abrolhos submarine platform of that height.

Oscillations of the sea both above and below its present level have clearly marked the last few thousand years. For some time there occurred the "climatic optimum" of the so-called Atlantic phase, when one would naturally expect a high eustatic sea-level, which now stood at 10 feet above the present sea-level. And at about 500 A.D. or so, according to Teichert's estimate, the 10-foot platforms cut by that sea emerged to greet the historical period.

* * * * *

During the Würm exposure, the island must have stood up as a fairly high eminence, about 350 feet above sea-level. Deep-reaching karst erosion set in and the whole of this limestone mountain became riddled with sink-holes, underground streams, caverns, stalactite caves, and the like. It is probable that the margins of this table-topped moun-

tain were higher than the centre though the rim may well have had gaps in the north. We might compare such a terrain with that of Christmas Island today (see, for example, Andrews, 1899), or of many raised coral islands of the Pacific. In any case, a deep valley became scoured out on the northern side.

Thus, when the sea-level rose to 10 feet above its present level after the Flandrian transgression, this erstwhile mountain was almost drowned, permitting the sea to enter into the former valley and allowing corals to grow up from its floor and from the stumps of the old reefs at a great rate. Parts of the old platform were still somewhat exposed, however, and the four main areas were variously affected:—

1. The South-western Reef, exposed to the heavy southerly and westerly gales, became worn down mechanically, as well as chemically.
2. The Central Platform became mostly planed down to sea-level by chemical erosion, leaving a few relict islands behind.
3. The South-eastern Reef, being exposed to severe southerlies as well as diminished south-westerly and north-westerly winds from the lagoon side, accumulated layers of shingle to form shingle ridges. These have protected it to a great extent from chemical erosion, so that it is now the main island of the group.
4. The Northern Reefs were very much dissected during the Würm erosion, but from these isolated points fresh coral grew up in new patches, radiating from the various centres in a cauliflower pattern. Shingle swept in by the north-westerly winds accumulated on top of them to help form new islets.

* * * * *

This is where a more precise dating in the Abrolhos could begin. For this 10-foot erosion level is perfectly clear on all the older islands. It is associated with contemporary shell-beds in protected places; on the more exposed islands Teichert has described extensive systems of shingle beach ridges formed at this level.

Subsequent to the final emergence (about 500 A.D. perhaps) the sea-level has dropped step by step to its present level. At the Abrolhos Teichert had got the impression that this was a gradual process, but at Rottneest he reviewed this impression (1947*b*) having observed unmistakable traces of still-stand at 5-6 and 2-3 feet. Similar indications were noticed by Kuenen in the East Indies (1933), Crossland in the Red Sea (1907), and by other authors in many parts of the world. I, myself, have been able to confirm this at many points.

During this last emergence rapid chemical erosion in the lagoon (coupled with mechanical erosion in the South-western Reef) has kept pace more or less with the drop in sea-level, except for local relics, but in the South-eastern Reef area (Pelsart Island) and in the Northern Reef area (the Mangrove Islets) wind and sea have combined to keep up the supply of coral debris and to keep these islands above water.

4. *Islets.*

In the Pelsart lagoon, three types of islet are recognised: the old lagoon limestone type (*e.g.*, Middle Island), the younger coral limestone type (*e.g.*, Centre Islet in the western Mangrove Group), and the very youthful shingle and sand cay type (*e.g.*, Stick Island in the northern islets). In addition, there is the complex rim island, Pelsart itself, already described by Teichert.

5. *Reefs.*

In the Pelsart Group, two distinct types of reef are recognised: the living coral and coralline assemblage; and the old eroded limestone platforms, which may be cut in either old coral material or in old lagoon limestones.

An ability to identify one type from the other from the air or on air photographs is hoped to have economic value, when it is recognised that crayfish inhabit the living types of reef, but not the old eroded platforms.

6. *Winds and Growth.*

The group is believed to have been initiated as a ribbon reef, more or less coinciding with the present South-west Reef, and orientated NW-SE with incurving extremities, being very similar to the present northern Outer Barrier reefs of Queensland. Wind and wave contributed to build out cones of debris from these two wings, in north-easterly and easterly directions; these two ridges finally joined up at the north-east corner, to make an almost perfect equilateral triangle. The South-eastern Reef, however, has always tended to build up faster than the Northern, thanks to the greater southerly and south-easterly elements in the wind directions. We thus have an almost perfect triangular atoll, though today there are some gaps along the northern edge. It is probable that these gaps were cut down deeply and thus emphasised, by subaerial and fluvial erosion during the last (Würm) Glacial period, when the sea-level was probably approximately 55 fathoms below the present.

Live coral forming the source material for accretion under wind and wave, is found on most peripheral reefs, and living coral heads grow up from the floor in the northern parts of the lagoon. It is found all around the Mangrove Islets and in the "Maze" in the north-east, but is almost totally absent over large areas of the Central Platform, where physico-chemical conditions are unfavourable.

7. *Reef Erosion.*

Three aspects of reef erosion are considered: biological, mechanical, and chemical. Of the three the last is considered paramount. While the probable phenomenon of chemical solution of calcareous reef material by sea-water under special circumstances is already well recognised, a definite, though simplified explanation is now put forward. Under special physico-chemical conditions, often in company with special biochemical conditions, the amount of CO_2 in the surface waters on shallow reefs is believed to vary to such an extent that CaCO_3 is alternately precipitated by day from a supersaturated solution, and at

Finally, probably not more than a century ago, the sea-level ceased to drop and started to rise once more. Both new and old beach ridges are now being eroded back in places, and corals appear to be growing higher on some of the reef-flats.* Gutenberg (1941) has identified a positive 10 cm. per century rise in the universal mean sea-level by exhaustive analyses of world-wide tidal data, while Ahlmann (1946) and other glaciologists report a general recession of the glaciers and an amelioration of the polar climates during the last 100 years. Thorarinson (1940) calculated this rise due to glacial melting at 5 cm. per century, which is certainly evidence of the same order, while Marmer's tidal analyses from Baltimore (1943) show a rather larger figure for the last quarter century.

IV. CONCLUSIONS.

Detailed mapping of several types of small islands which are found in the lagoon and on the Northern Reefs of the Pelsart Group are correlated with evidence obtained by Teichert on Pelsart Island (on the South-east Reef) and in the other groups of the Abrolhos. Further observations on the reefs and submarine topography of the great central lagoon are studied in the light of the general plan and situation of the Pelsart Group near the edge of the West Australian continental shelf. Special attention is paid to constructional and destructional processes in controlling the development of the reefs. Eustatic variations in sea-level are recognised and correlated. Conclusions have been reached as follows:—

1. *Classification.*

The Pelsart Group represents, in general terms, an atoll, but it has had a very long and complex history. Its situation near the edge of a continental shelf distinguishes it geographically from oceanic atolls, but does not appear to institute any fundamental genetic difference in the reef growth.

2. *Origin.*

According to the present state of our knowledge, it appears that the building of the oldest visible reefs took place in one of the warm, late Pleistocene interglacial periods of high sea-level, the most likely being the Late Monastirian time of the Riss-Würm interglacial when the sea-level was 25 feet higher than it is today. At this time old coral and lagoon limestones were deposited. The actual birth of the reefs may well have been somewhat earlier.

3. *Later History.*

The group has subsequently suffered the experience of oscillating Pleistocene and Recent sea-levels common to stable areas in the world. Its own basement is regarded as highly stable, at least during Quaternary times. There is evidence of the mid-Recent 10-foot sea-level, as well as of two subsequent levels at 5-6 feet and 2-3 feet. These are indicated by benches, notches, shell beds, etc. Low sea-levels during the Würm cold period are less certain, but there is some indication of levels at 55, 40, and 15 fathoms and an early Recent one at 3 fathoms.

*This contemporary rise of sea-level appears to be just as truly eustatic as the earlier changes (see my letter to the "Geographical Journal," Jan./Feb., 1947, and also one from Dr. Teichert).

night with cooling and excessive liberation of CO_2 by algæ, etc., more limestone is dissolved.

8. *Future Work.*

Clearly a very great deal more is to be learned in the Abrolhos. This may well include the following types of investigation:—

- (a) Air survey: A complete air photo coverage is urgently required, for scientific, economic and charting purposes.
- (b) Palæontological research: Contemporary shelly faunas require study and comparison with those of the earlier stages represented in the Abrolhos and up and down the coast. Valuable climatological conclusions may result.
- (c) Structural: Much still remains to be done in the way of reef exploration, especially the structure of under-water reef caverns and tunnels, which probably have an important bearing on the biological environments of the area.
- (d) Drilling and Geophysical work: As long ago as 1896 Saville-Kent was appealing for a deep-bore to make up for the disappointment of the Funafuti bore. It is still hard to imagine a better place for exploring the base of the reef and of the continental shelf in general than at Middle Island in the Pelsart Group.

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PLATE I.

REEF GROWTH.

Fig. 1.—General view of a shallow coral pool on the inner reef in the Mangrove Group. Tips of branching *Acropora* have been killed by exposure to spring tides and bleached. Raised algal-covered rim of reef may be seen in the middle distance beyond which is a deep channel.

Fig. 2.—The same reef flat seen from a boat in the channel. The raised algal-covered rim may be seen in the foreground. Undercut cliffs and some mangrove (*Avicennia officinalis*) form the distant shore.

Fig. 3.—A large *Euphyllia* (four feet diameter) showing "micro-atoll" structure. Growth in the centre has been stopped at some time, presumably by exposure, only to be continued all around the perimeter, where the coral has grown up higher than the centre under favourable conditions (neap tides).

Fig. 4.—A typical *Acropora* fan in a coral pool. Note how the tips of each of the higher corallites are killed and bleached by exposure.

All the above photographs (by the author) were taken at low spring tide.



Fig. 1



Fig. 2

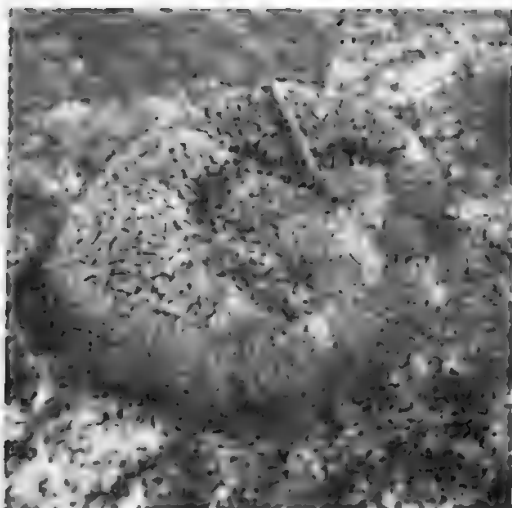


Fig. 3



Fig. 4

REEF LIMESTONE EROSION.

On the north-west side of Middle Island looking south-west. Typical undercut cliffs in the 10 foot lagoonal limestone. The upper surface of the latter is etched and eroded by rain-water solution, while its foot is undercut by sea-water solution. Note remnants of double notch and blackening above high tide line. Very little mechanical erosion occurs here as the shallow protecting reef-flat is several miles wide. The shallow reef-flat, seen below six inches of water, nearly at low tide, has no living coral, but is eroded out of a similar lagoonal limestone as the island. (Photo by the author).



PLATE III.

ERODED REEF FROM THE AIR.

The "Maze" at the north end of Pelsart Island. The living coral here appears only as a marginal fringe on the deeply indented margins or around pot-holes in the old coral or lagoon limestone platform which has been exposed at periods of low sea-level to severe erosion and is now almost submerged again. (Photo by R.A.A.F.)



2.—TWO NEW BERYLLIUM MINERALS FROM LONDONDERRY.

By

H. P. ROWLEDGE, A.W.A.S.M., A.A.C.I., and

J. D. HAYTON, B.Sc., A.A.C.I.*

Read: 12th November, 1946.

An examination of a specimen of brown cassiterite submitted by the Government Geologist from the feldspar quarry at Londonderry showed the presence of a dense compact mineral occurring in thin layers throughout the cassiterite. It could not be readily identified by optical means and there was insufficient material available for chemical tests.

At the authors' request for more material, Mr. H. A. Ellis, Government Geologist, visited the quarry and with the manager Mr. Duplex collected and forwarded more specimens of cassiterite-bearing pegmatite. Several large fragments were received containing wedge shaped pieces of cassiterite up to 3½ in. long and 2 in. across the base associated with quartz beryl and albite. The unidentified mineral called "A" occurred in thin layers 2 or 3 square inches in area lying on the cassiterite or closely adjacent to it and is the first mineral described in this paper.

Duplex drew Ellis' attention to another mineral associated with "A" in the specimens. It occurred as well crystallised colourless plates and fibrous prismatic radiating masses and is the second mineral described, called "B." Investigation has shown them both to be beryllium minerals new to Western Australia.

The Londonderry feldspar quarry is situated 13 miles S.S.W. by road from Coolgardie. Although a considerable quantity of pegmatite has been removed over a number of years while mining microcline, it was only recently that these new minerals were recognised. They occurred in a columbite-cassiterite band of mineralisation in the east wall in a second lower bench in the quarry.

"A" BOWLEYITE.

The first observed occurrence of this mineral showed it to occur as brownish white compact layers closely associated with cassiterite. A microscopic examination showed it to be intimately associated with fine granular quartz and a few scattered grains of cassiterite. The particles appeared to be uniform in character and were seen as colourless, flat plates, distinctly micaceous in habit, with weak birefringence, sometimes appearing isotropic.

* Mineralogist and Research Officer, and Mineral Chemist respectively, Government Chemical Laboratories, Western Australia.

In other later specimens it was seen to occur mainly in narrow narrow layers lying between quartz and wedge shaped masses of granular cassiterite and in small very thin layers throughout the cassiterite. It also occurred in massive form and as a lens shaped vesicular mass near to, but not in contact with, the cassiterite. These latter occurrences were associated with quartz to a much less extent and in some cases only a few grains were noticed under the microscope.

In all the samples of pegmatite examined, the similarity of appearance and the constant optical properties of the mineral indicated a uniform composition. It is infusible in the bunsen flame and when finely ground is decomposed by fuming sulphuric acid, with the separation of gelatinous silica.

The first sample for analysis was prepared from layers of the mineral as it was found *in situ* in the first observed occurrence. A microscopic examination of the powder showed it to contain a considerable amount of free quartz. This was determined by decomposing the mineral with fuming sulphuric acid and treating the residue with warm Lunge's solution to remove the separated silica. The free silica 34.27%, the small amount of SnO_2 present as cassiterite 0.13%, and moisture 0.20%, were deducted from the analysis and the balance recalculated giving the following figures:

Analysis	%	Mols.
SiO_2	32.22	5365
Al_2O_3	35.58	3490
Fe_2O_3	nil	—
BeO	8.05	3217
MnO	nil	—
MgO	nil	—
CaO	15.35	2737
Na_2O	.55	89
K_2O	.09	10
Li_2O	2.61	873
Ign. Loss	5.80	3219*
TiO_2	nil	—
P_2O_5	nil	—
Cl	nil	—
F	nil	—
CO_2	nil	—
Total	100.25	

S.G. Clean mineral 3.02

* Combined H_2O .

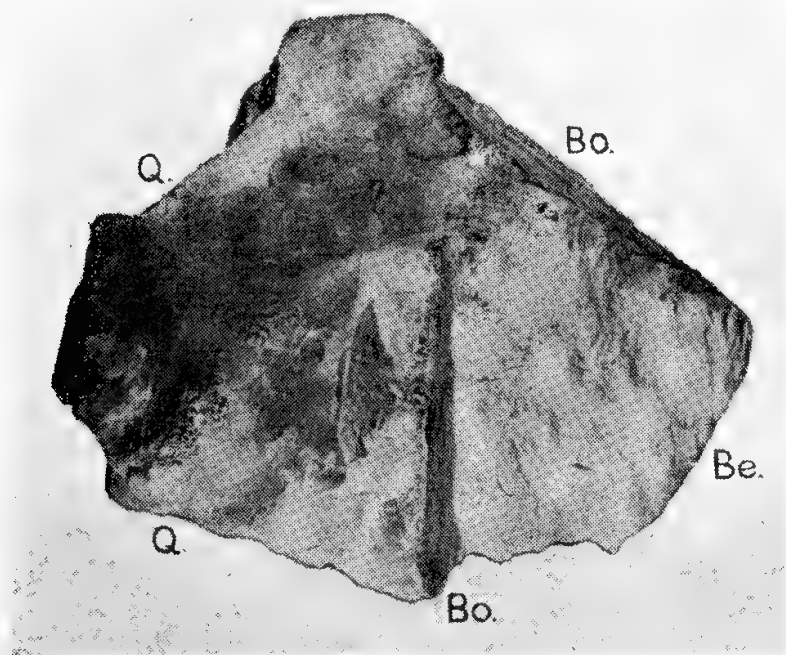
Analyst: J. D. Hayton.

At this stage of the investigation the authors visited the quarry to study the manner of occurrence and distribution and to collect further type specimens.

Unfortunately all the cassiterite bearing pegmatite had been removed and until further mining is done will not be exposed again. However an examination of spoil dumps from a nearby band of mineralisation containing columbite, yielded specimens of material which proved on examination in the laboratory to be the same mineral. Some good specimens were obtained which gave sufficient clean mineral for further examination. The optical and physical properties were the same as those obtained from the previous specimens examined.

In some specimens the mineral occurred as flat wedge shaped plates several square inches in area up to $\frac{1}{8}$ in. in thickness at the juncture of milky beryl and quartz and in fractures in the beryl itself (text fig. 1). It has quite definite lines of demarcation and does not appear to be an alteration product. It was also noticed as thin layers with thin plates of quartz, the surfaces of which formed a knife edge up to $1\frac{1}{2}$ in. long and in the centre of which is mineral "B" enclosing small idiomorphic crystals of quartz up to $\frac{1}{4}$ in. long. In other specimens it occurred as wedge shaped masses up to 2 in. in length and 1 in. across the base in pearly albite, beryl and quartz associated with small included patches of quartz and a little mineral "B."

Clean fragments of the mineral from one of the last specimens described free from quartz etc. were carefully selected by hand and lightly crushed to pass a 60 mesh screen. Any fines passing a 90 mesh screen were rejected. This -60 +90 product consisting of platy aggregates was then separated in bromoform solution, S.G. 2.84 to remove any small amounts of quartz, beryl, albite or mineral "B". The



Text fig. 1.—Bowleyite (Bo) at the junction of Beryl (Be) and Quartz (Q.). One-half natural size.

Photo. by S. E. Terrill,

heavy fraction from this separation was again separated in a solution S.G. 2.93 the heavy fraction of which being proved clean by microscopic examination was crushed to pass a 90 mesh screen for analysis.

Analysis	Moisture free	
	%	Mols.
SiO ₂	33.37	5556
Al ₂ O ₃	36.24	3555
BeO	7.30	2918
CaO	14.42	2571
FeO	.17	24
MnO	trace	—
MgO	.04	10
Li ₂ O	2.39	800
Na ₂ O	.29	45
K ₂ O	.04	4
Ign. Loss	5.72	3175*
TiO ₂	nil	—
Total	99.98	
	S.G. 3.03	

*Combined H₂O.

Analyst: H. P. Rowledge, J. D. Hayton.

The first analysis was carried out on selected fragments of the mineral as it occurred *in situ* without removing any impurities. The second analysis was done on the pure mineral after removing any small amounts of quartz, albite, beryl and mineral "B" present as described above. Both analyses give figures which are in reasonable agreement but the figures in the first were obtained by calculation after eliminating the quartz, the determination of which is not an exact method owing to the small possible attack of Lunge's solution on the quartz and the presence of any small amounts of other mineral unattacked by sulphuric acid. For the purpose of determining the true molecular constitution the figures from the second analysis must be taken as they represent the values on a clean sample.

The method adopted for the separation of beryllium and aluminium was based on the 8 hydroxyquinoline method described by Kolthoff and Sandell with later modifications by other workers and further modified by C. R. Le Mesurier at the Government Chemical Laboratories, Western Australia. The final method adopted has been successfully applied in the analysis of beryl in this laboratory and has been used in all analyses of beryl in this laboratory. It has been used in all analyses recorded in this paper.

The molecular ratios of the constituents shown by the analysis are:

SiO ₂	Al ₂ O ₃	BeO	Ca(Fe.Mg)O	Li(Na) ₂ O	H ₂ O
1	.64	.53	.47	.15	.57
		1.00			

The alkali molecules are in minor proportions and the authors are of the opinion that they are not an essential part of the constitution but are small amounts in excess in the mineralising solution over that required for the crystallisation of petalite and have been occluded in the mineral which is considered to be the last product of solidification in the process of differentiation.

Beryllium oxide is assumed to be isomorphously replaceable with calcium oxide and eliminating the alkalis the principal constituents are in the ratio of $3[\text{BeCa}(\text{FeMg})]\text{O} \cdot 2\text{Al}_2\text{O}_3 \cdot 3\text{SiO}_2 \cdot 2\text{H}_2\text{O}$, with the ratio of $\text{BeO}:\text{CaO}$ approximating 1 : 1.

The formula for this mineral would thus be $3[(\text{BeCa})\text{O}] \cdot 2\text{Al}_2\text{O}_3 \cdot 3\text{SiO}_2 \cdot 2\text{H}_2\text{O} + n \text{Li}(\text{Na})_2\text{O}$.

An optical examination of the powder showed it to consist of colourless micaceous plates normal to Bxa or nearly so. The maximum and minimum refractive indices of the plates on the flat lie between 1.65 and 1.66, with very weak birefringence. On edge the maximum refractive index was greater than, but near to 1.66, the birefringence being about that for quartz. The mineral is biaxial negative with 2E small.

Conclusions.

The predominant form in which this mineral occurs is in brownish white, flat compact waxy looking layers and in wedge shaped micaceous aggregates associated with quartz, beryl, albite and mineral "B" in the columbite and cassiterite bearing bands of mineralisation in the pegmatite.

In different parts of the east wall of the quarry where these occur, are individual masses of minerals containing the elements found in the mineral with the exception of lime. Lithium and aluminium occur as petalite, beryllium and aluminium as beryl. The feldspars are albite and microcline, the soda and potash varieties respectively. It is interesting to note that no lime minerals other than the mineral under discussion have yet been recognised in this pegmatite.

The method of occurrence of mineral "A" suggests that it is the last product of crystallisation of the mineralising solution. It is different in chemical composition, optical and physical characteristics from any known mineral and is therefore a new species for which the name *Bowleyite* is given in honour of Mr. H. Bowley, Director of Chemical Laboratories and Government Mineralogist of Western Australia.

"B" DUPLEXITE.

Mineral "B" occurs as fan shaped crystalline aggregates up to $\frac{1}{2}$ in. in radius sometimes forming almost complete rosettes. It is pearly white and lustrous, extremely brittle with pronounced cleavage in two directions. When crushed it breaks into long and short rectangular fragments. Some of these fragments show very weak birefringence, sometimes appearing isotropic, while the majority show moderate to weak birefringence and have a small extinction angle ($2-5^\circ$). The splinters

are readily fusible in the bunsen flame. The powder is insoluble in strong hydrochloric acid or fuming sulphuric acid.

The fragments for the first analysis were carefully selected by hand, crushed and cleaned by separation in known S.G. solutions. Bromoform S.G. 2.84 was first used to separate any heavy minerals including mineral "A". The light fraction was then separated in a bromoform-acetone mixture S.G. 2.67 to separate any quartz or possible kaolin. A microscopic examination of this heavier fraction showed some slight alteration of mineral "B" and the absence of quartz. It was again separated in solution S.G. 2.63. The coarser particles of this heavier fraction were again lightly crushed and separated as before. The final product S.G. > 2.63 < 2.75 was examined and crushed through a 90 mesh screen for analysis.

The second sample was prepared from another specimen in which the mineral was more plentiful and clean. A number of small fragments were carefully selected and crushed. The first powdery crushings -90 mesh were discarded as they appeared more cloudy than subsequent fractions. The remainder was crushed through a 90 mesh screen and used for the second analysis.

Analysis.	1.		2.	
	%	Mols.	%	Mols.
SiO ₂	58.92	9810	59.13	9845
Al ₂ O ₃	6.88	675	7.00	687
Fe ₂ O ₃	.07	4	nil	—
BeO	7.72	3085	7.14	2854
CaO	23.26	4148	23.90	4262
MnO	.01	1	.01	1
MgO	.13	32	.05	12
Na ₂ O	.44	71	.10	16
K ₂ O	.04	4	nil	—
Li ₂ O	trace	—	nil	—
Ign. Loss	n.d.	—	2.46*	1366
H ₂ O+	2.41	1337	n.d.	
H ₂ O-	.06		.06	
TiO ₂	nil		nil	
P ₂ O ₅	nil		nil	
SnO ₂	nil		nil	
F	nil		nil	
Cl	n.d.		.02	
CO ₂	n.d.		.03	
C	n.d.		.11	
Total	99.94		100.01	

S.G., 2.71.

Analyst: J. D. Hayton.

*Ignition Loss, taken as combined water, after deducting .11C, .02 Cl, .03 CO₂, .06H₂O.

The molecular ratios of the principal constituents are as follows:

	SiO ₂	BeO	Ca(MgMn)O	Al ₂ O ₃	H ₂ O
Anal. 1	1	.30	.43	.07	.14
" 2	1	.29	.43	.07	.14

The formula for this mineral would thus be—



A microscopic examination of the powder showed it to have the following optical properties:

Ng 1.593, Nm 1.584, Np 1.582 Na, Ng-Np = .011.

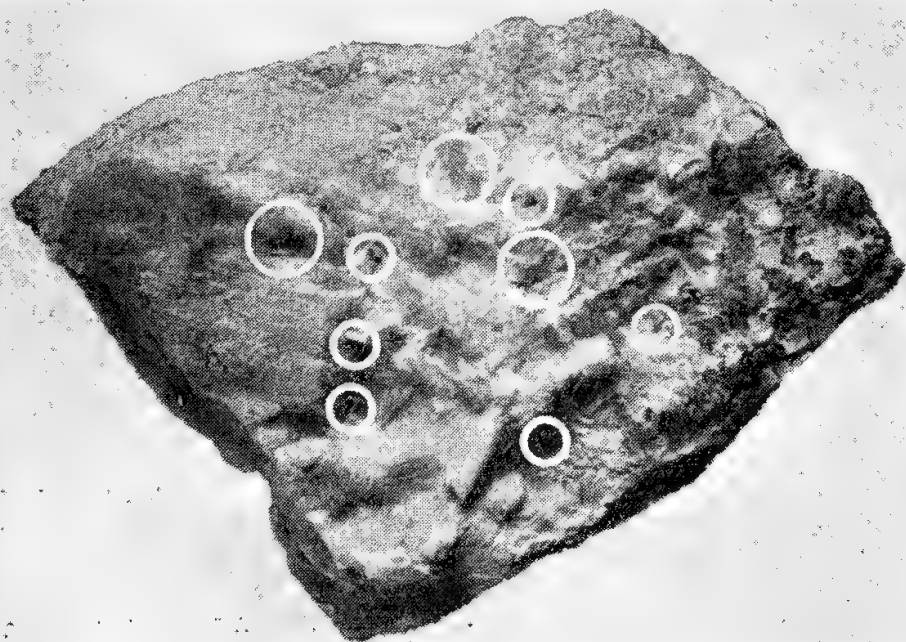
Biaxial +, 2V approx. 22°.

Elongation Negative. Extinction Angle 2-5°.

Conclusions.

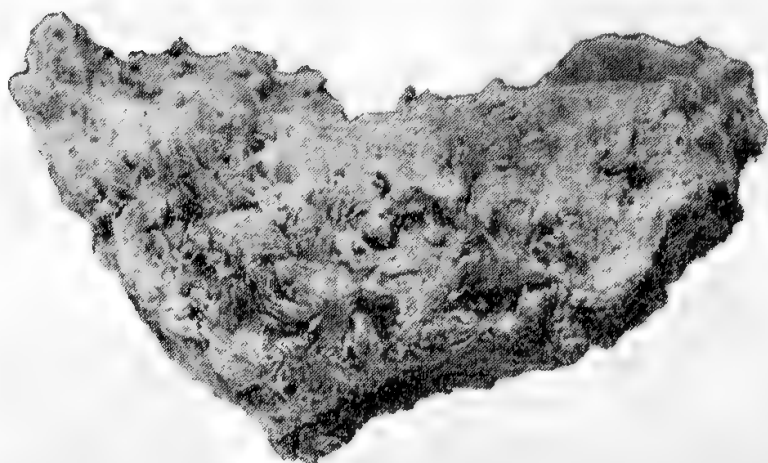
The first specimen examined showed the mineral as occurring in fibrous radiating crystalline aggregates forming numerous rosettes over an area of several square inches abutting mineral "A" and associated with quartz, albite and beryl.

Other specimens showed it as well crystallised squarish plates penetrating a cavity surrounded by radiating fibrous and platy masses bordered by a rectangular plate of quartz. Embedded in the mineral were smaller plates of quartz. The remainder of the specimen consisted of partly altered milky beryl. On one edge was a small wedge of cassiterite and in places thin films of pucherite. Another specimen showed it as



Text fig. 2.—Radiating crystals of duplexite enclosing idiomorphic quartz crystals (in circles). Two-thirds natural size.

Photo. by S. E. Terrill.



Text fig. 3.- Platy crystal aggregates of duplexite in beryl, quartz, albite, pegmatite. Two-thirds natural size.

Photo. by S. E. Terrill.

typical radiating masses over an area of 3 or 4 square inches in which were embedded small well developed quartz crystals the largest being approx. $\frac{1}{2}$ in. long. (text fig. 2).

The manner of occurrence suggests that the mineral was one of the last to crystallise from the mineralising solution penetrating the pegmatite and that it has crystallised at the same time as or later than the idiomorphic quartz crystals, but before Mineral "A."

In optical properties it closely resembles bavenite as described by Schaller and Fairchild which contains 2.67% BeO with a molecular ratio for $\text{Al}_2\text{O}_3:\text{BeO}$ of 1:1. This ratio was also obtained by Grill in a new analysis of bavenite from Baveno. Mineral "B" however, contains 7.14% BeO with a molecular ratio for $\text{Al}_2\text{O}_3:\text{BeO}$ of 1:4. No mineral is yet known with the composition as shown by the analysis and it is a new species for which the name *Duplexite* is suggested, after the manager of the quarry, Mr. S. Duplex, who first drew attention to this mineral.

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3.—A GRAZING INCIDENCE METHOD FOR THE DETERMINATION OF HIGH REFRACTIVE INDICES.

By

S. E. TERRILL, B.Sc., A.A.C.I.

Read: 11th March, 1947.

The determination of the refractive indices of minerals is usually done indirectly. The refractive index of a liquid or fusible solid medium is made to agree with that of the mineral and the index of the medium is then determined.

Fragments of the mineral are immersed in the medium and their refractive indices compared, using a polarizing microscope. The comparison is effected by well-known Becke Line or shadow methods, or by means of special methods such as that described by Saylor (1935). Suitably oriented grains are selected by optical methods (Slawson and Peck, 1936) or else grains are made to lie in the desired position by use of a universal stage. The refractive index of the medium is commonly changed by mixing two selected media, one with a higher refractive index than the mineral and the other a lower index: the proportions are varied until the index of the mixture matches that of the mineral grain. The refractive index of the immersion medium may be varied by other means; the wave-length of light (Posnjak and Merwin, 1922) or the temperature (Gaubert, 1922), or both the wave-length of light and the temperature may be varied (Winchell and Emmons, 1926). Whatever method is adopted for matching the refractive index of the immersion medium to that of the mineral, there still remains the determination of the refractive index of the medium at the temperature and for the wave-length of light used.

A search of mineralogical literature has shown that the refractive indices of immersion media of high refractive index are almost universally determined on a goniometer by Fraunhofer's method of minimum deviation. A hollow prism is used for liquids and solid media are moulded between cover-slips to form prisms.

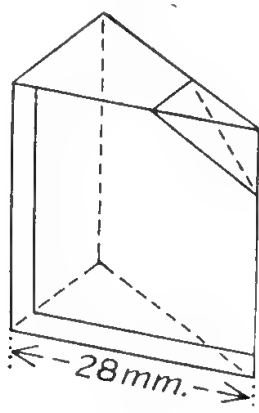
Of the several methods available for determining refractive indices with a prism, there are two that are especially suitable for use with the goniometer, namely, Fraunhofer's method of minimum deviation already mentioned and Kohlrausch's method of critical or grazing incidence. It appears that the latter method has been overlooked entirely by mineralogists: it offers certain advantages of speed and convenience over that commonly employed, and an accuracy satisfactory for most mineralogical purposes is easily obtained with the simplest accessories on any goniometer which can be read to one minute of arc.

An advantage that may appeal to some is that the instrument can be used without disturbing it from its adjustment for the examination

of crystals. Another point of appeal is that, unlike the determination of the position of minimum deviation, only one reading of each position of the prism is necessary, these positions being ascertained with ease and precision.

While a sodium lamp or flame is desirable and indeed seems necessary in the high ranges of solid media, values which are quite satisfactory for purposes of identification can be obtained for liquid media using an ordinary white light, making all adjustments to the yellow-green portion of the spectrum.

The hollow prism used by the author has a refracting angle of fifty degrees, while another of forty degrees is also available. These are made after the pattern used by Ross, described by Larsen (1921): the solid prism has one corner of the refracting edge bevelled off to form the hollow prism when two one-inch square portions of good quality microscope slide are cemented to the solid prism with deKhotinsky's cement, as shown in text fig. 1. No attempt was made to select the glass by interference methods, checking for parallelism of perfectly flat surfaces; the only check made was to observe the undistorted reflection of a straight edge of a window, first from one surface and then the other. For other than room temperatures, a prism similar to that described by Butler (1933) can be used.



Text fig. 1. A simple hollow prism.

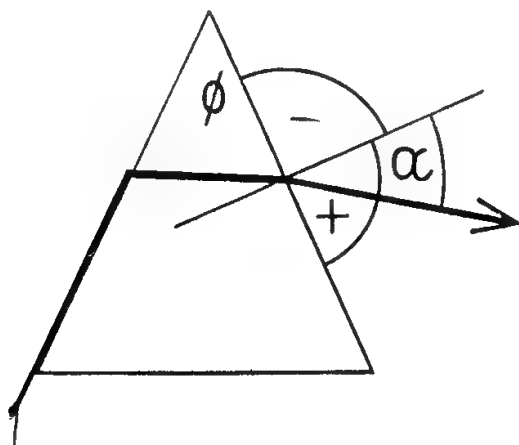
Hollow prisms of such simple pattern have been found to be quite stable and may be sluiced repeatedly with alcohol and dried in a blast of cold air without altering the refracting angle; consequently a graph can be drawn for each prism used, saving much of the time taken in calculating the refractive indices from the data obtained.

Prisms of solid media are made by melting the medium into the angle between two pieces of thin microscope slide; number one cover-slips were found to be too thin, as they distort too readily as the melt solidifies. The other chief difficulty in obtaining prisms of solid media, that of obtaining a clear rather than a frosted refracting edge, is best overcome by being sufficiently liberal in the use of the medium.

In the intermediate range of refractive indices, from 1.55 to 1.67, indices determined by this method with such simple accessories as

described were compared with those obtained on the same liquids using an Abbe refractometer made by Hilger: they were found to differ by not more than 0.0002. Lacking any means of direct comparison for the high ranges, a series of determinations was run on thallium bromide, one of the solid media to which attention has been drawn by Barth (1929): the average was 2.425 and the maximum deviation therefrom was 0.006. Barth gives 2.42 as the refractive index of this medium.

The principle of the method is illustrated in text fig. 2. Light from a sodium-lamp impinges at grazing incidence upon the incident face of the prism and is refracted into the prism and again refracted upon passing through the emergent face. The angle between the direction of emergence of the light and the normal to the emergent face of the prism is measured; this angle, and the refracting angle of the prism, constitute all the data necessary for the calculation of the refractive index.



Text fig. 2. The path of light at grazing incidence.

The equation relating the refractive index of the prism to the refracting angle and the angle of emergence, that is, the angle between the emergent light beam and the normal to the emergent face, can be cast into the form

$$n = \sqrt{\left(\frac{\cos \phi + \sin \alpha}{\sin \phi} \right)^2 + 1}$$

where n = refractive index of the prism,

ϕ = refracting angle of the prism,

α = critical angle of emergence, that is, the angle between the normal to the emergent face and the position of emergence at grazing incidence.

The critical angle of emergence, α , is positive if in the quadrant between the normal and the base, as shown in text fig 2, and negative if between the normal and the refracting angle.

For those who use the popular Goldschmidt two-circle goniometer, an outline of the method as developed by the author at the Government Chemical Laboratories, Perth, for application to the instrument as made by Stoe & Cie, m.b.h., is given here. Suitable modifications are readily made to apply the method to other types and to single-circle goniometers.

Assuming the instrument to be in adjustment, the steps in the determination are as follow:—

- (1) Set up the prism in the goniometer so that the refracting edge is parallel to one of the plane slides and vertical, and so placed that the plane of the incident face clears the vertical circle (the horizontal-axis graduated circle).
- (2) Set the prism so that both the vertical axis of the instrument and the telescope axis pass through it, using the carriage slide and the plane slides.
- (3) Set the refracting edge of the prism parallel to the vertical axis of the instrument.
- (4) Measure the refracting angle of the prism.
- (5) Determine the position of the normal to the emergent face.
- (6) Determine the position of critical emergence.
- (7) From (5) and (6) derive the critical angle of emergence and calculate the refractive index, using the equation given above.

The first two steps are fairly straight forward, requiring but little ingenuity in mounting the prism. This is cemented to its supporting peg or pin in such a way that the prism is perched high above the horizontal axis of the peg; the incident face of the prism then comes above the level of the horizontal rocking screw arc which otherwise would cast a shadow on it. The plane of the incident face is made to clear the vertical graduated circle by means of the horizontal rocking screw.

Having set the telescope lenses to give an enlarged image of the target, which combination is used throughout the determination, the refracting edge is made parallel to the vertical axis in the usual way so that, no matter which face of the prism reflects the target, its image remains on the horizontal cross-hair.

If a series of refractive indices is being determined, the prism may be re-set accurately in its holder after each cleaning by first setting it vertical, as near as can be, by eye, and then turning it about the vertical axis to bring the reflection of the target into the field of the telescope; if off-centre, loosen the clamp slightly, turn the prism about its supporting peg until the image is centred and re-clamp firmly. If carefully done, much time can be saved, for the prism can be set in the same

position every time: it becomes necessary then only quickly to check the setting and the position of the normal to the emergent face.

To determine the position of the normal to the emergent face, the same arrangement is used as for adjusting the telescope by auto-collimation. The prism is swung until the image of the cross-hairs reflected from the emergent face of the prism coincides with the direct image. In this position the axis of the telescope is normal to the emergent face; the horizontal circle is read and noted as the position of the normal.

The sodium lamp is placed at the same distance as the target from the vertical axis and at the same height and in such a position that the light from it reaches the incident face of the prism at a moderate angle, some ten to thirty degrees or so, from the direction of the base of the prism. The prism is swung about the vertical axis until a sharp image of the lamp is seen in the telescope. Retaining the image of the lamp in the field and keeping the lamp at the same distance from the vertical axis, move the lamp towards the plane of the incident face, swinging the prism as necessary. This causes the image of the lamp to become attenuated, so much so that finally it becomes the merest streak of light. This streak is placed behind the vertical cross-hair. The horizontal circle is read, noting this as the position of critical emergence.

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4.—ANATOMY OF THE QUOKKA [*Setonix brachyurus* (Quoy and Gaimard)]

PART I.—EXTERNAL MORPHOLOGY AND LARGE INTESTINE.

By
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Read: 10th June, 1947.

INTRODUCTION.

A.—GENERAL.

The quokka (*Setonix brachyurus*) is a diprotodont marsupial of the family *Macropodidae*. Its body is about as big as that of a large cat, but the whole animal is rather squat and has not the graceful appearance of the larger members of the family. In certain attitudes it looks very like an enormous rat, particularly when it is feeding on some loose object such as an apple, when the food, resting on the ground is held between the forelimbs, the whole body being outstretched and close to the ground (pl. 1).

The animal is now almost confined to Rottnest Island which is 11½ miles west of Fremantle, but, according to Shortridge (1909 p. 813) it once was "Very plentiful among coastal thickets and swamps of the South-West, not extending inland" and it also occurred "sparingly as far north as Moore River." He further noted that it is not found on Garden Island but recorded it from ". . . Bald Island to the east of King George's Sound, and on Twin Peak and probably other islands off Esperance." Troughton (1941, p. 196) and Glauert (1934, p. 32) give similar accounts of its distribution.

Dutch navigators of the 17th century who landed, more by chance than intention, in a few places on the west coast of Australia or on outlying islands, noticed animals which were probably or certainly quokkas. The first published record is, according to Troughton (1941, p. 197), by Samuel Vlockersen, who, in 1658, mentioned a ". . . wild cat resembling a civet cat, but with brown hair."

On December 30, 1696, van Vlaming and his men landed on a large island. "On exploring it they were struck with the large number of rats' (wallabies') nests to be seen and gave it the name of 'Rottnest Island.'" (Battye, 1924, p. 40).

One of Vlaming's party wrote regarding Rottnest Island, "There are very few birds there and no animals, except a kind of rat as big as a common cat, whose dung is found in abundance all over the island." (Major, 1859, p. 121).

The quokka was identified by the French naturalist Bailly and others in 1801 as a "small species of Kangaroo" (Glauert, 1929, p. 38) but was first systematically described by Quoy and Gaimard (1830, pp. 114-116). The specimen, which had been found dead at King George Sound, was named *Kangarus brachyurus*. Wood Jones (1924a, p. 261) indicates that the generic name *Setonix* was given to it by Lesson, 1842.

B.—POSITION OF *SETONIX* IN THE FAMILY MACROPODIDAE.

The quokka differs from most other macropods in dentition, having large sectorial pre-molars and small, low-crowned molars. This was recognised, figured, and recorded, together with some external measurements and the character of the skull, by Thomas (1888, p. 60).

Bensley (1903) has discussed at length the phylogenetic relationships of the marsupials. In the case of *Setonix*, he recognises the resemblance between its pre-molars and molars, and those of the Tree Kangaroo (*Dendrolagus*) and of *Dorcopsis*. However, he suggests that, through the loss of the canines and the purely terrestrial character of the foot, it is probably a member of the group of Small Wallabies of genus *Macropus*; it has paralleled *Dendrolagus* in its feeding habits. (1903, pp. 151-152 and p. 202.)

Troughton (1941, p. 196) recognises the peculiarity of the dentition of the quokka and its resemblance to that of the Tree Kangaroo (*Dendrolagus*) and of the *Dorcopsis* Wallabies, but he places it with *Thylogale* under the general heading "Scrub or Pademelon Wallabies."

Wood Jones (1924a, pp. 220 and 261) places the animal in the brachydont section of the sub-family *Macropodinae*; this section includes *Dendrolagus* and *Dorcopsis*, which *Setonix* resembles in the nature of its pre-molar and molar teeth, but from which it differs in having no canine teeth and in having a very short tail, scarcely twice the length of the head—whence, of course, its specific name "brachyurus."

Lydekker (1894, pp. 41-42) and Le Souef and Burrell (1926, pp. 175-176 and 200), apparently not realising the significance of the quokka's dentition, place it in the genus *Macropus* and seemingly in the sub-genus *Thylogale*, which would be correct if one relied solely on externals and neglected the dentition.

According to Wood Jones (1923, 1924a) the quokka's position in the animal kingdom is:—

Class Mammalia.

Sub-Class Didelphia.

Order Marsupialia.

Sub-Order Sydactyla.

Section Syndactyla Diprotodontia.

Family Macropodidae.

Sub-Family Macropodinae, brachydont section.

Genus *Setonix*.

Species *brachyurus*.

C.—PURPOSES AND METHOD OF THIS STUDY.

Apart from the observations of Bensley and Thomas there is no published information on the general characteristics and habits of *Setonix*, except Fleay's article (1936, pp. 153-155) dealing with its birth habits, nor has anything been written about the anatomy of its soft parts. Beddard (1908 p. 568) does indeed give measurements of the intestine, but does not describe it.

This paper is intended to be the first part of a fairly detailed discussion of all anatomical systems of *Setonix*, which should be the basis for comparison with local macropods and with other members, *Dendrolagus* and *Dorcopsis*, of the brachyodont section of the sub-family Macropodinae. Such comparisons may throw further light on the relationships of *Setonix*.

A single adult male specimen of the Garden Island Wallaby [*Macropus* (*Thylogale*) *eugenii derbianus* (Gray)], which will be called *Macropus eugenii* throughout this paper, became available towards the end of the investigation. References have been made to *M. eugenii* in the text and a section has been included dealing briefly with the pattern of its hindgut, comparing it with that of *Setonix*.

Until it is possible for full comparisons to be made between *Setonix* and other macropods, it seems well to report in detail on the external features and hindgut of the seven specimens available so that full information would be provided for future comparisons. The examination of a number of specimens should, to some extent, preclude the drawing of false conclusions regarding the typical anatomy of *Setonix*, due to individual peculiarities and variations.

Two dead pouch embryos, one 70 millimetres and the other 110 millimetres from tip of snout to base of tail, were recovered from specimens in my possession. Notes on the ileo-coecal and colic regions of these embryos have been made enabling comparisons to be drawn between them and adults. Further details of the 110 millimetre specimen are given on p. 143 under IV ("Notes on the Natural History of the Quokka").

Some observations of natural history have been made on the living animals and these, together with a problem regarding the insular distribution of the Garden Island Wallaby and the Quokka, are included as Section IV at the end of the paper.

Many of the figures included in this paper were prepared by placing the specimen about 9 inches below a 3' x 2' frame, subdivided by cords to give a 25 mm. square mesh. The particular structure was drawn on to graph paper ruled into 5 mm. squares.

This investigation, part of the course for an Honours B.Sc. degree in the University of Western Australia, was carried out under the supervision of Professor G. E. Nicholls, while I was the recipient of a Hackett Research Scholarship.

In addition, my thanks are due to Mr. L. Glauert, Curator of the Perth Museum, to Mr. K. Sheard, of C.S.I.R. Division of Fisheries, and

to Mr. E. P. Hodgkin, Lecturer in Zoology at the University of Western Australia, for kind help and advice in the preparation of this paper. I also wish to thank the Rottnest Board of Control for permission to obtain specimens, and Mr. N. Love, of Rottnest, who very kindly obtained and forwarded to me three male and three female specimens which were all adult or approaching adulthood (see p. 63), thus adding to my own collection of one small immature male. Some of the specimens were kept alive and in good health in a large cage at the Department of Biology of the University of Western Australia.

II.—EXTERNALS.

A.—INTRODUCTION.

Description of externals in a normal animal may be an important pre-requisite to physiological research on the animal. This is made apparent by the recent work of Bolliger (1938, 1943 a and b, 1946) on the changes in integumental structures of *Trichosurus vulpecula*, resulting from the administration of sex hormones and gonadotropin. If similar work is ever carried out on *Setonix*, familiarity with the externals in their normal, healthy state would be invaluable in detecting any change in them after treatment of the animal with the above compounds. Particularly important, in this respect, would be a knowledge of the colour, length and concentration of hair, and of any pigmentation of the skins, in the region of the pouch, scrotum and cloacal orifice.

The general form and appearance of the quokka have been described already (p. 59). (See also pl. 1.) Apart from differences in actual, and in some cases, of relative size, the external morphology of *Setonix* does not appear to differ in any important particular from that of other macropods.

Much of what I describe of the externals, particularly the pelage, has been recorded by Quoy and Gaimard (1830, p. 114), Waterhouse (1846, p. 162), Thomas (1888, pp. 60-61), but the inclusion of figures, not given in earlier descriptions and illustrating certain external features, will perhaps justify some repetition.

The tables of measurement and ratios emphasise features some of which have been recognised in past descriptions of single specimens.

The condition of the premolars has been taken as the criterion of adulthood in this investigation. At least one animal (specimen 3, female) in my collection was sexually mature, as indicated by the presence of an embryo in the pouch, but I consider that, judged by its dentition, it was not strictly adult. Though sexual maturity may be just as legitimate a base from which to measure ages, it is not as practical as the condition of the teeth.

From an examination of my specimens and of skulls of *Setonix* in the collections of the Department of Biology in the University of Western Australia, it seems that there is in the right and left upper and lower jaws of the young animals, a *milk* sectorial premolar. This is 4 mm. long and has two shallow vertical grooves about 0.5 mm. apart and placed at about the middle of the length of the tooth, running from

its cutting edge towards the gum. In the adult this tooth is replaced by a larger *permanent* sectorial premolar, 6 mm. long and with three shallow grooves.

Thus, by examination of the sectorial premolar of *Setonix* its *dental* age can be determined. In this respect those with the shorter, milk sectorial premolars are regarded as immature, those with the longer permanent sectorial premolars as mature.

Specimens 2, 5, 6, and 8 were mature, 1, 3, and 4 were immature in their premolar dentition.

Specimen 1 (a small male) was not included in measurements.

In describing the externals of *S. brachyurus* I have largely followed Finlayson (1930, pp. 47-56, 1932, pp. 148-67), and Wood Jones (1920, pp. 360-73; 1922, pp. 119-30; 1923; 1924a; 1924b, pp. 145-8).

B.—METHODS OF MEASUREMENT USED IN THIS PAPER.

All measurements have been made to the nearest millimetre.

1. *Total Body Length.*

The specimen was straightened out without unnatural stretching, and the length taken with a cord from the tip of the snout to the base of the tail, following the curves of the mid-dorsal line (Finlayson, 1930, p. 55; Wood Jones, 1923, p. 12). By flexing the tail at right angles to the body, its base was better defined.

2. *Measurements on Head.*

All measurements were made with calipers. Measurements a. to e. were used by Finlayson (1932, p. 165, Table 1). In addition the recording of the maximum transverse width of the head and the width of the head at the base of the ears, is suggested by Thomas' statement (1888, p. 61) that the skull of *Setonix* is strongly built and broad in proportion to its length.

a. Rhinarium to eye.

From tip of rhinarium to anterior canthus of eye.

b. Eye.

Canthus to canthus.

c. Eye to ear.

From posterior canthus of eye to notch between tragus and antitragus of ear.

d. Length of ear.

From notch between tragus and antitragus to tip of ear (see also Wood Jones, 1923, p. 13, fig. 10).

e. Breadth of ear.

Maximum breadth, without distortion, of external ear from its cephalic to its caudal margin.

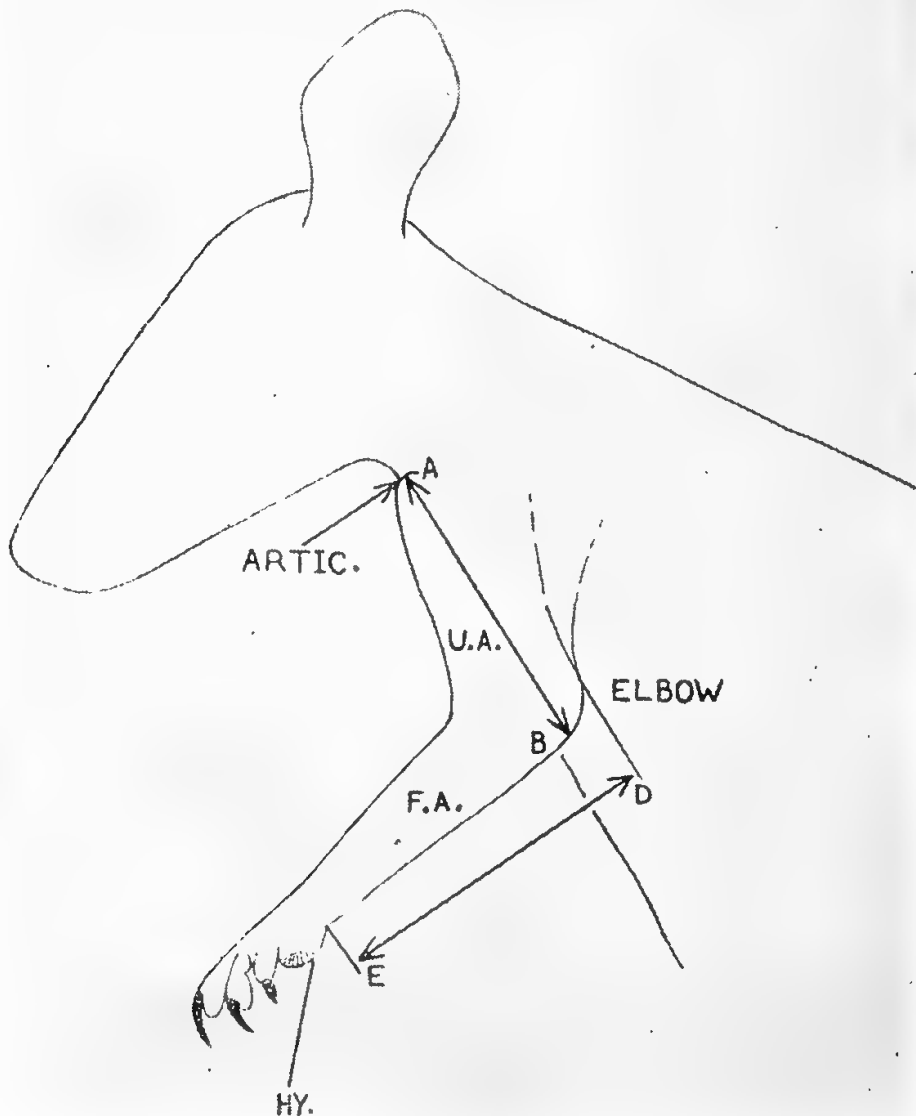
f. Maximum transverse width of head.

Corresponds roughly to articulation of lower jaw with upper.

- g. Transverse width of head at base of ears.
Between inflated areas of the cartilaginous portion of external auditory meatus near base of ear.

3. *Measurements on Forelimb.*

All these were made with calipers. Finlayson (1930, p. 55, Table 1) lists the length of the "humerus" and "ulna radial length." These appear in a table with flesh measurements and so presumably were made in the flesh, despite the use of skeletal names. In the same table c. and f. of the measurements detailed below are given. The statement by Waterhouse (1846, p. 162) that the forefeet of *Setonix* are proportionately rather large suggests the additional measurements of the breadth of the hand and length of the third finger.



Text fig. 1.—*S. brachyurus*. Lateral semi-diagrammatic view of head and shoulders to show length A-B of upper arm and D-E of fore arm.

ARTIC.—region of articulation of humerus with scapula;
F.A.—forearm; HY—hypothenar pad; U.A.—upper arm.

- a. Length of upper arm.
Taken from articulation of humerus with scapula to the elbow. (text fig. 1). The articulation could be felt through skin and muscle.
- b. Length of forearm.
Taken from elbow to proximal end of hypothenar pad on palm of manus (text fig. 1).
- c. Length of hand.
Taken from proximal end of hypothenar pad to tip of third digit, excluding the nail.
- d. Breadth of hand.
Taken from preaxial base of first finger to postaxial base of fifth finger.
- e. Length of third finger.
Taken from line joining base of the cleft between 3rd and 2nd, and 3rd and 4th fingers to the tip of finger, excluding nail.
- f. Length of claw of third finger.
From base to tip.

4. *Girth of Chest.*

This measurement was used by Finlayson (1930, p. 55, table 1; 1932, p. 165, table 1). It is the maximum girth of the thorax, taken with a cord, in the diaphragmatic region.

The measurement is not very satisfactory because there is no very definite external point from which it can be taken. I also tried taking the measurement at a point defined by reference to the ribs, but this did not seem any more satisfactory.

5. *Measurements on hind limb.*

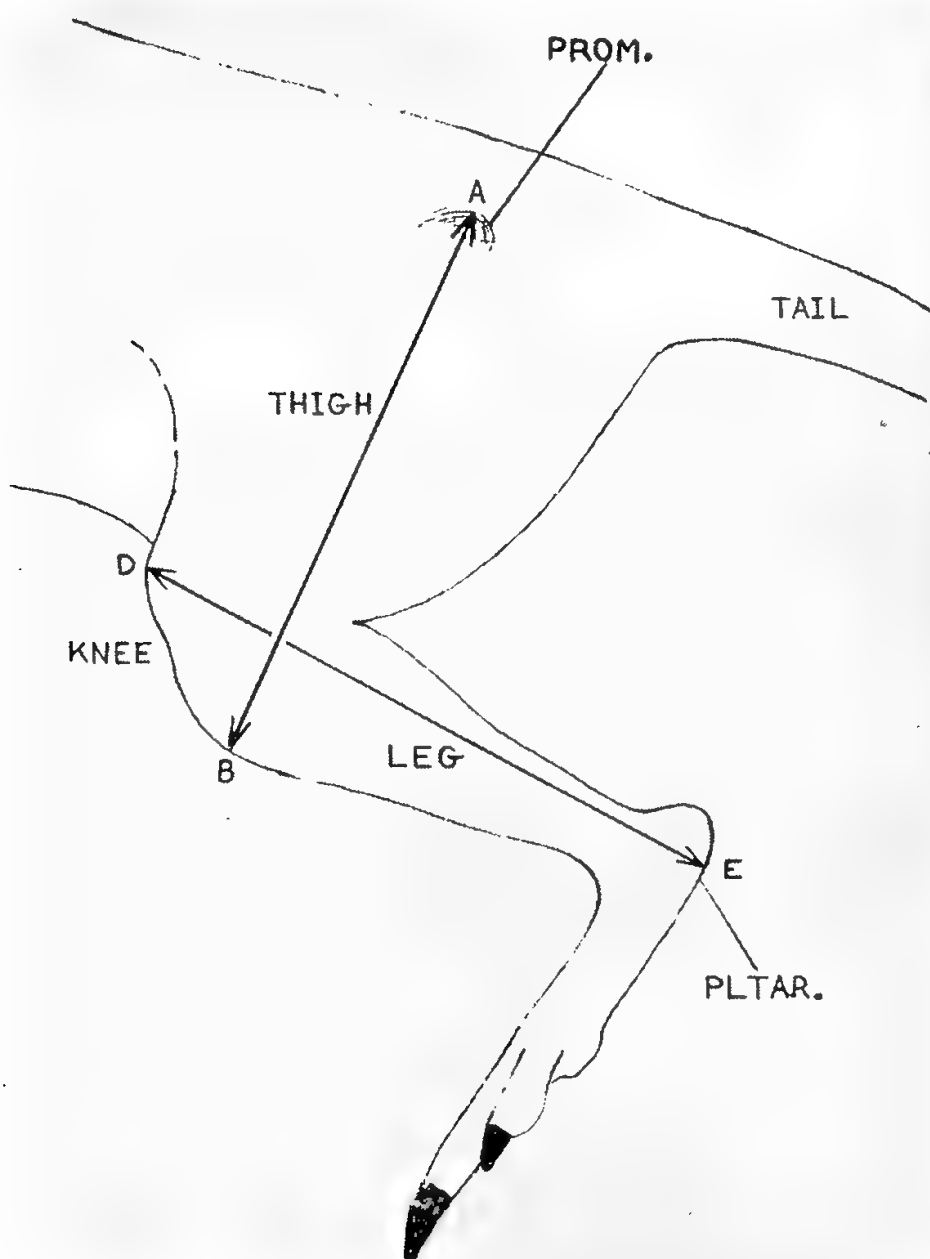
All these were made with calipers. Finlayson (1930, p. 55, table 1) gives the lengths of "femur" and "tibia," and I have made the same assumption regarding them as I did for "humerus" and "ulna-radial" above; he also gives measurements for c, d, e, and for which I give results.

- a. Length of thigh.
Taken with thigh flexed at right angles to leg, from region of acetabulum in which the great trochanter could be felt, to knee (text fig. 2).
- b. Length of leg.
Taken with leg flexed at right angles to thigh and to foot, from knee to plantar surface of heel (text fig. 2). The measurement therefore includes portions of thigh and foot; in spite of this, the points between which the measurement is taken are more satisfactory than others which might give the true length of the leg.
- c. Length of foot.
Taken from "the point of the heel to the tip of the most distant

toe, but the claw must not be included in the measurement." Wood Jones, 1923, p. 12 and fig. 9). The most distant toe in this case is the fourth.

d. Breadth of foot.

Bensley (1903, p. 175) takes this measurement in a pentadactyl animal such as *Perameles* across the foot immediately behind the hallux. There is no hallux in the quokka, so the measure-



Text fig. 2.—*S. brachyurus*. Lateral semi-diagrammatic view of hind-quarters to show length A-B of thigh and D-E of leg.

PLTAR.—Plantar surface of heel; PROM.—prominence (? great trochanter).

ment is taken across the foot from preaxial base of syndactylous toe to postaxial base of fifth toe.

e. Length of fourth toe.

Taken from base of cleft between the fourth and fifth toes to tip of fourth toe, excluding nail.

f. Length of claw of fourth toe.

Taken from its base where it joins the fourth toe to its tip.

6. *Measurements on tail.*

a. Length of tail.

As indicated in the tables of measurements and ratios, both Wood Jones's and Finlayson's have been employed (Wood Jones, 1923, p. 12, fig. 9; Finlayson, 1930, p. 55). Owing to the ill defined nature of base of tail even when tail is flexed at right angles to body, Wood Jones's does not seem as satisfactory as Finlayson's, which has for its proximal point the posterior margins of cloaca, which are better defined than base of tail.

b. Girth of tail.

Taken at its base which, as already stated, is not well defined, so that this measurement is rather unsatisfactory.

Specimen Number	6	5	4	7	3	2
Sex	♂	♂	♂	♀	♀	♀
Total Length	527	488	465	500	465	537
Rhinarium to Eye	40	40	38	34	34	38
Eye—Canthus to Canthus . . .	13	13	13	11	11	15
Eye to Ear	43	43	42	40	40	45
Length of Ear	42	40	43	44	39	37
Breadth of Ear	30	30	32	30	28	27
Maximum Width of Head . . .	53	52	53	51	51	54
Width of Head at Base of Ears	41	45	46	35	43	45
Length of Upper Arm	69	64	68	57	55	58
Length of Forearm	83	80	83	75	70	73
Length of Hand	30	29	36	31	30	32
Breadth of Hand	16	15	20	15	15	15
Length of 3rd Finger	13	11	15	11	11	12
Length of Claw of 3rd Finger . .	9	9	9	10	7	9
Girth of Chest	272	272	317	263	263	270
Length of Thigh	121	115	116	112	102	111
Length of Leg	145	144	127	143	128	135
Length of Foot	108	110	112	102	101	105
Breadth of Foot	17	19	21	19	16	18
Length of 4th Toe	34	33	36	34	32	34
Length of Claw of 4th Toe . . .	21	17	11	16	13	16
Length of Tail (Finlayson) . . .	332	337	350	313	288	321
Length of Tail (Wood Jones) . .	294	320	321	292	258	302
Girth of Tail	102	113	106	110	84	90
Weight in lbs. (preserved specimens)	5¼	5	6½	5¼	5	7

TABLE I.—Body Measurements (in millimetres) on *S. brachyurus*. Details of dental age of specimens, see p. 63.

Specimen No.	1
Sex	♂
Total Length	590
Rhinarium to Eye	57
Eye—Canthus to Canthus	15
Eye to Ear	47
Length of Ear	64
Breadth of Ear	35
Maximum Width of Head	55
Width of Head at Base of Ears	46
Length of Upper Arms	100
Length of Forearm	114
Length of Hand	45
Breadth of Hand	25
Length of 3rd Finger	17
Length of Claw of 3rd Finger	15
Girth of Chest	397
Length of Thigh	151
Length of Leg	233
Length of Foot	144
Breadth of Foot	23
Length of 4th Toe	45
Length of Claw of 4th Toe	25
Length of Tail (Finlayson)	509
Length of Tail (Wood Jones)	471
Girth of Tail	180
Weight in lbs. (preserved specimen)	13½

TABLE II.—Body measurements (in millimetres) on *M. eugenii*.

C.—EXAMINATION OF MEASUREMENTS.

Measurements were completed before I had thought of comparing the measurements of males and females of *Setonix* or of using this method of comparing *Setonix* with other macropods.

The following is an analysis of these measurements, but the results can only be regarded, at the best, as suggestions.

1. *Source of error in flesh measurements.*

Apart from the "personal equation" these are:—

a. State of preservation.

In this investigation all specimens had been preserved in museum fluid for various periods up to two months prior to measurement, and therefore soft tissues, in contrast to skeletal structures, may have been distorted, the amount of distortion differing in the various specimens.

b. Lack of definite landmarks.

The points between which measurements were taken were often not sharply defined, definition varying from specimen to specimen. This lack of definiteness is particularly apparent in measuring the length of body, made with reference to the ill-defined base of tail, in measuring the basal girth of tail and the length

of upper arm and thigh (head of humerus and great trochanter are sometimes difficult to find beneath the muscles).

c. "Give" of tissues.

A less important source of error than a. or b. is the yielding of tissues under the pressure of calipers.

Possibly the most satisfactory of all the flesh measurements, being least affected by the sources of error as set out above, is the length of the foot.

2. *Method of examination.*

In order to compare lengths in males and females of *S. brachyurus* and between them and the one specimen of *M. eugenii* measurements were converted into ratios by both—

- a. dividing each measurement of a set for a given specimen, by the foot measurement of that specimen,
- b. dividing each measurement of a set for a given specimen, by the total body length of that specimen.

It is considered that (a) is more satisfactory than (b)—Hersh (1941) and Lumer, Anderson & Hersh (1942) have indicated that it is desirable in such comparisons, to take as a base measurement which corresponds to the animal's total length at some fixed event within the animal's life history. It is thought that the length of the foot in the adult *Setonix* is reasonably related to the suspected body length at the time of its emergence from the pouch, that is, at the end of the "infant stage," a definite event in the growth cycle.

Adult body length is reached towards the end of the growth period and its use as a base may produce false ratios.

As stated earlier, it has been found that measurement of the length of the foot is also more satisfactory from the point of view of accuracy of measurement, than body length.

In testing for possible differences between either male and female of *Setonix* or between male and female *Setonix* and *M. eugenii* the following method was employed, which was considered adequate for such a small investigation as this involving a very few specimens; more involved statistical analysis with its conclusions, could well be very misleading. If the range of ratios for a given measurement on, say, male specimens of *S. brachyurus* does not overlap or fall within the range of ratios for the same measurement in females, then this is regarded as suggesting a difference, i.e. a sex difference, in the relative lengths of the particular structure measured, but no conclusions for or against a sex difference can be drawn if the range of ratios for that particular measurement for males overlaps or falls within that for females.

The same principle was observed in testing for possible differences between *S. brachyurus* and *M. eugenii*.

In some cases the difference between the range of ratios for a male and female specimen of *Setonix* is very small, in others it is large. By taking a bigger sample the range of ratios for one sex may overlap, or

There is a possible sex difference in:—

- i. Maximum width of head—that of female being the wider.
- ii. Length of upper arm—that of male being the greater.

The ranges of all other ratios for male and female either overlap or fall within each other and in such cases conclusions have not been made.

- b. From Table V. (measurements for any one specimen divided by its body length).

The following are greater in male than in female:—

- i. Length of rhinarium to eye.
- ii. Length of upper arm.
- iii. Length of forearm.
- iv. Length of thigh.

The ranges of all other ratios for male and female either overlap or fall one within each other and in such cases conclusions have not been made.

4. *Suggested differences between S. brachyurus and M. eugenii.*
(Measurements for any one specimen divided by its foot length.)

- a. From Tables III and IV.

The following are greater in *M. eugenii* than in *S. brachyurus*:—

- i. Length from rhinarium to eye.
- ii. Length of ear.
- iii. Length of upper arm.
- iv. Length of forearm.
- v. Length of leg.
- vi. Length of tail (Finlayson and Wood Jones method).
- vii. Girth of tail.

The following are smaller in *M. eugenii* than in *S. brachyurus*:—

- i. Total length.
- ii. Eye—canthus to canthus.
- iii. Eye to ear.
- iv. Breadth of ear.
- vii. Length of tail.
- v. Maximum width of head. There is a sex difference in this ratio in *Setonix*. The relative maximum width of head in *M. eugenii* is smaller than in either male or female *Setonix*.
- vi. Width of head at base of ears.

The ranges of all other ratios for *M. eugenii* fall within those for *Setonix* and in such cases no conclusions have been made.

	Combined Range	♂	♀
	♂ & ♀		
Total Length	4.15—5.11	4.15—4.88	4.60—5.11
Rhinarium to Eye	0.33—0.37	0.34—0.37	0.33—0.36
Eye—Canthus to Canthus	0.11—0.14	0.12	0.11—0.14
Eye to Ear	0.37—0.43	0.37—0.40	0.39—0.43
Length of Ear	0.35—0.43	0.36—0.39	0.35—0.43
Breadth of Ear	0.26—0.29	0.27—0.29	0.26—0.29
Maximum Width of Head	0.47—0.51	0.47—0.49	0.50—0.51
Width of Head at Base of Ears	0.34—0.43	0.38—0.41	0.34—0.43
Length of Upper Arm	0.54—0.64	0.58—0.64	0.54—0.56
Length of Forearm	0.69—0.77	0.73—0.77	0.69—0.73
Length of Hand	0.26—0.32	0.26—0.32	0.29—0.30
Breadth of Hand	0.14—0.18	0.14—0.18	0.14—0.15
Length of 3rd Finger	0.10—0.13	0.10—0.13	0.11
Length of Claw of 3rd Finger	0.07—0.10	0.08	0.07—0.10
Girth of Chest	2.47—2.83	2.47—2.83	2.57—2.61
Length of Thigh	1.01—1.12	1.04—1.12	1.01—1.10
Length of Leg	1.13—1.40	1.13—1.34	1.27—1.40
Length of Foot	1.00	1.00	1.00
Breadth of Foot	0.16—0.19	0.16—0.19	0.16—0.19
Length of 4th Toe	0.30—0.33	0.30—0.32	0.32—0.33
Length of Claw of 4th Toe	0.10—0.19	0.10—0.19	0.13—0.16
Length of Tail (Finlayson)	2.85—3.12	3.06—3.12	2.85—3.07
Length of Tail (Wood Jones)	2.55—2.91	2.72—2.91	2.55—2.88
Girth of Tail	0.83—1.08	0.94—1.03	0.83—1.08

TABLE III.—Ratios—obtained by dividing each measurement made on a given specimen of *S. brachyurus* by a foot measurement of that specimen (see p. 69). The range only of such ratios for a given measurement on males or females is shown.

may diverge even further from, the corresponding set of ratios for the other sex. No allowance for this, nor any prediction as to which differences suggested here would be eliminated by examination of larger samples, has been made. This proviso applies also to examination for possible differences between *M. eugenii* and *S. brachyurus*.

In making comparisons, the ratios for male and female specimens were examined for any sex difference. Following this, comparisons between *S. brachyurus* and *M. eugenii* were made. If it had previously been found that, for any one measurement there may be a sex difference in the quokka, then comparisons were first made between the males of that animal and *M. eugenii* (male). Further, if the ratio for a given measurement in *M. eugenii* did not fall within the whole range for the same measurement in both male and female quokkas, then it was considered that a difference between both male and female quokkas and the male of *M. eugenii* was suggested.

Ratios in which there is no indication of a sex difference in *Setonix*, were compared as a whole with the same ratios for *M. eugenii*.

3. Suggested difference between male and female.

- From Table III. (measurements for any one specimen divided by its foot length).

Specimen No.	1
Sex	♂
Total Length	4.10
Rhinarium to Eye	0.40
Eye—Canthus to Canthus	0.10
Eye to Ear	0.33
Length of Ear	0.44
Breadth of Ear	0.24
Maximum Width of Head	0.38
Width of Head at Base of Ears	0.32
Length of Upper Arm	0.69
Length of Forearm	0.79
Length of Hand	0.31
Breadth of Hand	0.17
Length of 3rd Finger	0.12
Length of Claw of 3rd Finger	0.10
Girth of Chest	2.76
Length of Thigh	1.05
Length of Leg	1.62
Length of Foot	1.00
Breadth of Foot	0.16
Length of 4th Toe	0.31
Length of Claw of 4th Toe	0.17
Length of Tail (Finlayson)	3.53
Length of Tail (Wood Jones)	3.27
Girth of Tail	1.25

TABLE IV.—Ratios obtained by dividing each measurement made on *M. eugenii* by its foot measurement.

	Combined Range	♂	♀
	♂ & ♀	♂	♀
Total Length	1.00	1.00	1.00
Rhinarium to Eye	0.07—0.08	0.08	0.07
Eye—Canthus to Canthus	0.02—0.03	0.02—0.03	0.02—0.03
Eye to Ear	0.08—0.09	0.08—0.09	0.08—0.09
Length of Ear	0.07—0.09	0.08—0.09	0.07—0.09
Breadth of Ear	0.05—0.07	0.06—0.07	0.05—0.06
Maximum Width of Head	0.10—0.11	0.10—0.11	0.10—0.11
Width of Head at Base of Ears	0.07—0.10	0.08—0.10	0.07—0.09
Length of Upper Arms	0.11—0.15	0.13—0.15	0.11—0.12
Length of Forearm	0.14—0.18	0.16—0.18	0.14—0.15
Length of Hand	0.06—0.08	0.06—0.08	0.06
Breadth of Hand	0.03—0.04	0.03—0.04	0.03
Length of 3rd Finger	0.02—0.03	0.02—0.03	0.02
Length of Claw of 3rd Finger	0.01—0.02	0.02	0.01—0.02
Girth of Chest	0.50—0.68	0.52—0.68	0.50—0.57
Length of Thigh	0.21—0.25	0.23—0.25	0.21—0.22
Length of Leg	0.25—0.29	0.27—0.29	0.25—0.29
Length of Foot	0.20—0.24	0.20—0.24	0.20—0.22
Breadth of Foot	0.03—0.04	0.03—0.04	0.03—0.04
Length of 4th Toe	0.06—0.08	0.06—0.08	0.06—0.07
Length of Claw of 4th Toe	0.02—0.04	0.02—0.04	0.03
Length of Tail (Finlayson)	0.60—0.75	0.63—0.75	0.60—0.63
Length of Tail (Wood Jones)	0.55—0.69	0.56—0.69	0.55—0.58
Girth of Tail	0.17—0.23	0.19—0.23	0.17—0.22

TABLE V.—Ratios obtained by dividing each measurement made on a given specimen of *S. brachyurus* by the total body length of that specimen (see p. 69). The range only of such ratios for a given measurement on males or females is shown.

- b. From Tables V and VI (measurement for any one specimen divided by its body length).

The following are greater in *M. eugenii* than in *S. brachyurus*—

- i. Length from rhinarium to eye.
- ii. Length of ear.
- iii. Length of upper arm.
- iv. Length of forearm.
- v. Length of thigh .
- vii. Length of tail (Finlayson and Wood Jones method).
- viii. Girth of tail.

In i, iii, iv, and v there is a sex difference in *Setonix*, and, in each case, the corresponding ratio in *M. eugenii* is greater than that for either sex in *Setonix*.

There is only one measurement—maximum width of head—which is relatively smaller in *M. eugenii* than in *Setonix*.

The ranges of all other ratios for *M. eugenii* fall within those for *Setonix*, and in such cases no conclusions have been made.

5. Conclusion.

It has been emphasised that the sample of animals available for this investigation was small and consequently conclusions drawn from observations on differences in ratios between the sexes of *Setonix* and between *Setonix* and *M. eugenii*, merely suggest that further work on much larger samples of each genus may be of value in discovering definite differences between the two genera and between the sexes.

D.—EXTERNAL MORPHOLOGY AND HAIR.

General colour of dorsal surface of body, grey-brown; that of ventral surface a lighter silver-grey. Hairs of dorsal surface rather coarse, those of ventral surface finer.

1. Head.

a. Hair.

Hairs of head shortest towards tip of muzzle and longest towards ears. Largely of a rufous colour, reaching maximum intensity laterally in region of mystical and submental sets of vibrissae, and at bases of ears. On dorsal surface there is a smaller number of grey and dark brown or black hairs mixed with rufous ones. Ventral surface of lower jaw covered with light grey hairs.

b. Form (Pl. I and II; text fig. 3).

Head shaggy in appearance and may be more conical than the heads of larger macropods. (See suggested differences in relative lengths and breadth of head of *M. eugenii* and *S. brachyurus*. From region of maximum width, between eyes and ears, it tapers rapidly and uniformly to rhinarium. Profile from rhinarium to

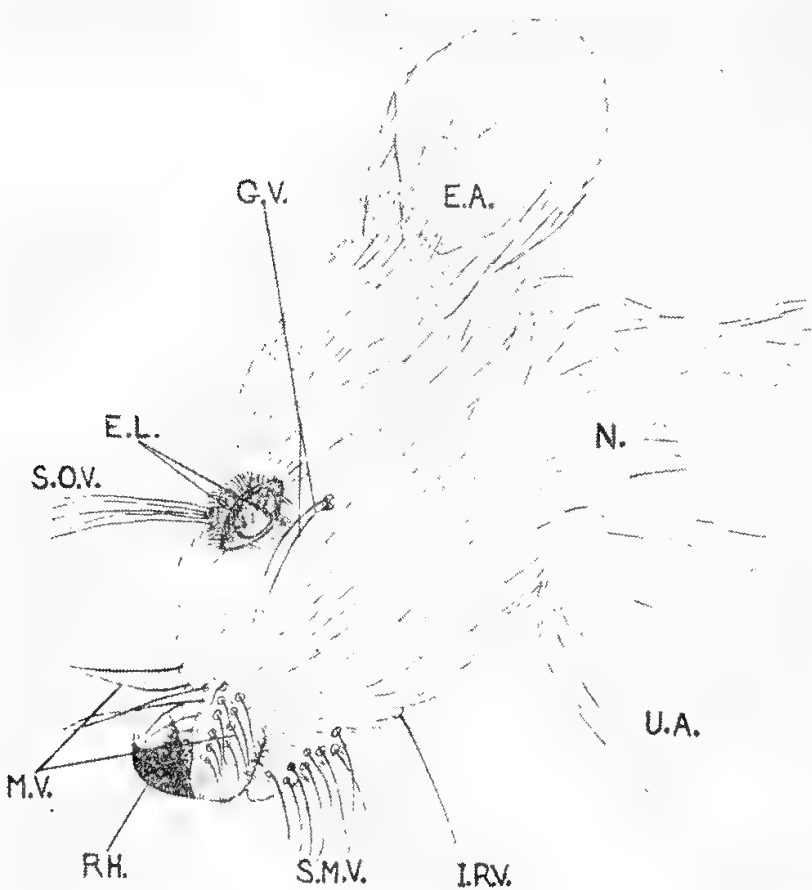
ears fairly flat; there is no convexity between the eyes (supra-orbital or frontal regions).

The interorbital region of two *skulls* examined is, in fact, slightly concave. In keeping with this uniform tapering, the muzzle is not abruptly truncated but has a rather rounded tip (see pl. I and text fig. 3).

c. Rhinarium (text fig. 4).

Rhinarium dark brown or black, relatively large and well formed and distinctly marked off from rest of hair-covered muzzle. It is up to 17 mm. in depth, 13 mm. in breadth and extends about 7 mm. along muzzle. It extends slightly on to dorsal surface of face, whereas in *M. eugenii* it does not. Rhinarium of *M. eugenii*, smaller.

Rhinarium of quokka has a small, rounded, median projection from its caudal and dorsal margin. This projection, which is directed caudad along muzzle, is about 1 mm. long and 3 to 4 mm. wide at its base, where it joins the rest of the rhinarium. Nostrils crescentic in outline; there is a median cleft extending



Text fig. 3.—*S. brachyurus*. Lateral view of head. $\frac{3}{4}$ natural size. E.—eye; E.A.—external ear; E.L.—eyelashes; G.V.—genal vibrissae; I.R.V.—interramal vibrissa; M.V.—mystical vibrissae; N.—neck; RH.—rhinarium; S.M.V.—sub-mental vibrissae; S.O.V.—supra orbital vibrissae; U.A.—upper arm.

about half way up rhinarium. Cleft widens towards the oral margin of upper lip, exposing anterior upper pair of incisors. Rhinarium continuous with upper lip by way of two narrow bands of naked skin, separated by median rhinal cleft.

Rhinarium hairless, its surface granular or tessellated; tesserae largest in middle line and diminish in size towards margins of rhinarium.

d. Eye. (text fig. 1).

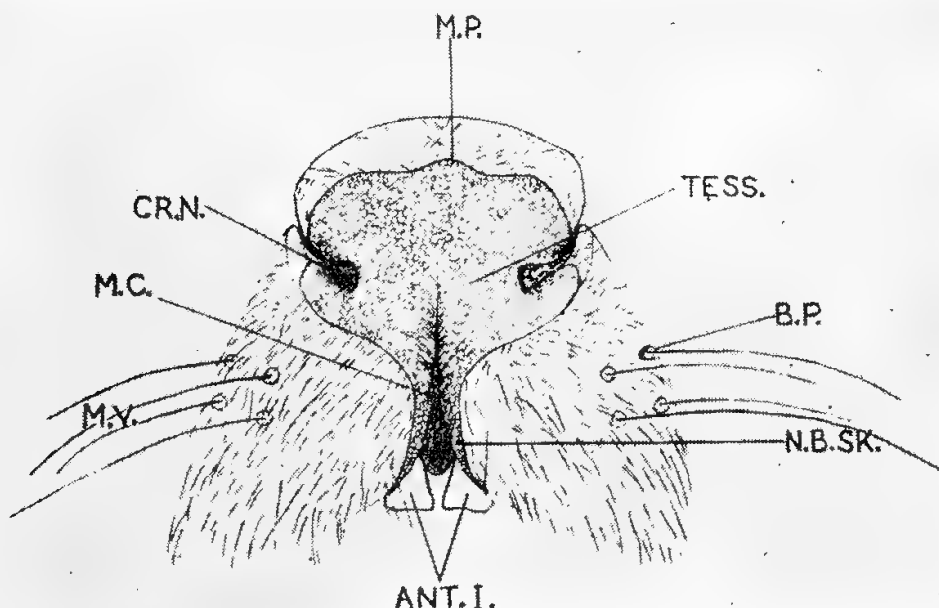
Each eye is 11 to 15 m.m. long, measured from canthus to canthus. Iris dull dark brown, eyelashes black, those of upper eyelid being the longer, their maximum length being 10 mm.

e. External ear (text fig. 5).

Inner and outer surfaces of external ear covered with red hairs; those of inner surface softer and finer than those of outer.

The short and rounded form of the external ears of *Setonix* is strikingly different from the elongate ear characteristic of the genus *Macropus* (Wood Jones, 1924a, p. 234, and also my suggested differences in relative length and breadth of ear of *M. eugenii* and *S. brachyurus*, p. 71).

Following Cunningham (1937, p. 101) and Wood Jones (1923, p. 7 and fig. 2), the concha shows a well developed tragus, an antitragus and an antihelix. Antitragus not as well developed as tragus, which is partly separated from rest of cephalic (dorsal) part of helix by a small notch. Between tragus and antitragus is a larger notch. Antihelix is a low ridge within concha, near,



Text fig. 4.—*S. brachyurus*. Rhinarium shown in relation to surrounding hair-clad muzzle. 2 x natural size.

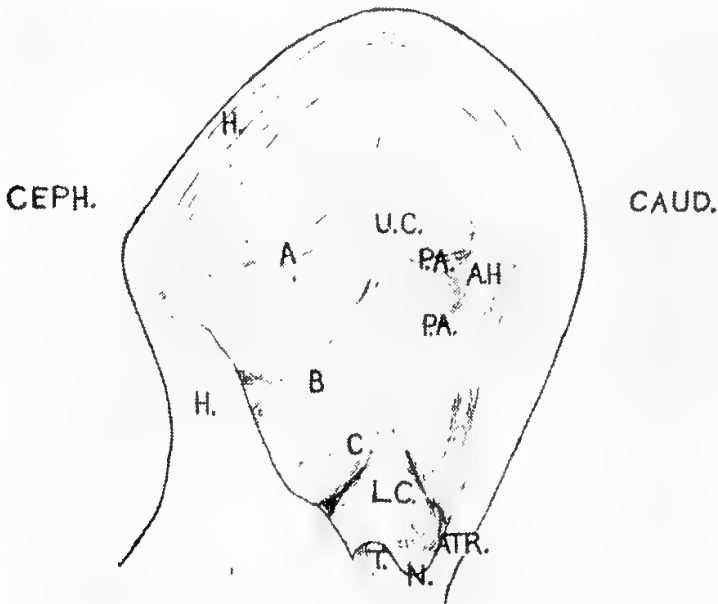
ANT. 1.—1st pair of upper incisors; B.P.—basal papilla of a mystical vibrissa; CR.N.—crescentic nostrils; M.C.—median cleft of rhinarium; M.P.—median projection of rhinarium; M.V.—mystical vibrissa; N.B.SK.—narrow band of naked skin between rhinarium and upper lip; TESS.—tesserae covering rhinarium.

and approximately following outline of caudal (ventral) margin of external ear. As secondary processes of the anti-helix there are at least two processi antiheliciis, which are short and run from the antihelix towards the cephalic margin of ear; they terminate in the region of the mid-longitudinal axis of ear. There are also three other secondary processes within the concha. Two of these (B and C in text fig. 5) are well developed and lie in the lower cephalic half of concha. At their cephalic end they appear to merge into the helix: towards their caudal ends they become low and, fanning out, merge into the general inner surface of the concha; both approach the processi antiheliciis, the low caudal end of B being closer to them than that of C.

The third secondary process (A in text fig. 5) is a low, ill defined ridge, variable in the amount of its development. It loses its identity cephalad before reaching the helix; caudad it fans out over surface of concha, so that in part it tends to be continuous with caudal end of B. It does not approach the antihelix or its processi as closely as does B.

Though A, B, and C do not appear to arise in the adult from the antihelix, they may possibly be regarded as processi antiheliciis.

There is no bursa developed in the caudal margin of the helix.



Text fig. 5.—*S. brachyurus*. Left external ear showing processes developed within concha. Hair covering external ear omitted. $1\frac{1}{2}$ x natural size.

A, B and C—see p. 76; A.H.—antihelix; ATR.—antitragus; CAUD.—caudal (ventral) margin; CEPH.—cephalic (dorsal) margin; H.—helix; L.C.—lower part of concha leading to external auditory meatus; N.—notch separating tragus from helix; P.A.—processi antiheliciis; T.—tragus U.C.—upper part of concha.

f. Facial vibrissae (text figs. 3 and 4).

All groups of facial vibrissae, which are regarded by Wood Jones (1923, p. 7) as typical of mammals, represented, though some are better developed than others. Vibrissae generally distinctly thicker and stiffer than other non-sensory hairs covering head. Each arises from a basal, grey coloured, papilla about 0.5 mm. in diameter.

It seems that, in keeping with the general darker colour of hair of upper surfaces of body as contrasted with the lighter coloured hair of lower surfaces, the vibrissae of dorsal and dorso-lateral aspects of head are dark brown, those of ventro-lateral and ventral aspects are lighter coloured, so that, for instance, the inter-ramal vibrissae is almost silver grey.

- i. Mystical set.—Most extensive and best developed set. It is quite distinct, being on either side of tip of muzzle, occupying an area about 10 m.m. square, of which the cephalic margin is about 10 mm. from tip of muzzle, and the upper (dorsal) margin about 10 mm. below dorsal surface of muzzle. Each vibrissa directed laterally from its point of origin. There are four longitudinal rows of papillae with their associated vibrissae. The rows decrease in definition dorsad, and above the last distinct row, there may be additional unorientated papillae with vibrissae arising from them. The vibrissae, which reach a maximum length of about 25 mm., are dark brown or black in the upper rows, and of a lighter shade in the lower (oral) rows.
- ii. Submental set.—This is a well developed, distinct set on the right and left margins of lower jaw. Vibrissae dispersed over an area about 10 mm. long and 5 mm. deep, the cephalic margin of which is about 10 mm. from tip of lower jaw; they are directed down and out from their points of origin, and number about nine in each area. They are a light shade of brown and reach a maximum length of about 15 mm., being the shortest vibrissae of face.
- iii. Interramal set.—This is unpaired and seems very poorly developed, for it was seen only in two of the six specimens examined. In the two—an adult male and an adult female—there is a single vibrissa arising from a distinct papilla situated in the middle line of lower jaw and about 25 mm. from its tip. Vibrissa is almost silver grey, directed downwards from its point of origin, reaching a length in the male of 30 mm. and in the female of 20 mm.
- iv. Supraorbital set.—This is small but distinct, the basal papillae being packed close together to form, as it were, one large papilla about 3 mm. long and 2 mm. wide. The set is on each side of head about 3 mm. above eye and 2 mm. behind its posterior canthus. Vibrissae, about four in number, dark brown or black and directed out and up from their basal papillae. Maximum length about 25 mm.

- v. Genal set.—This is a small set, and, as with the supraorbitals, its basal papillae are packed closely together so as to give the impression that there is but one large papilla, about 2 mm. in diameter on which smaller papillae are superimposed. The set lies on either side of head, about 10 mm. below and 4 mm. behind posterior canthus of eye. It has two or three strongly developed vibrissae, which have a maximum length of about 35 mm. Each is dark brown or black and is directed out and slightly back from its basal papilla.

2. *Hairs of thorax.*

Shoulders covered with rufous hairs and a smaller number of gray and dark brown (black) hairs. Rufous area of shoulder roughly triangular (isosceles) in shape, apex of triangle pointing caudad and base of triangle stretching transversely across shoulder from forelimb to forelimb. Extent of this rufous area of shoulder varies, if not with sex, then with condition of animal; its apex may be half way along dorsal aspect of body.

Dorsal surface of thorax therefore slightly rufous; lateral surfaces grizzled grey.

3. *Fore limb.*

a. *Hair.*

Because of lateral extension of rufous area of shoulder, hairs covering the outer surfaces of upper arm and forearm (animal orientated as in pl. I) largely light rufous with a smaller number of slate-grey and brown hairs mixed with them. Inner surfaces, as with all ventral aspect of body, light (silver) grey. Hair of forearm becomes shorter towards its distal end. Back of hand covered for about 10 mm. with short, dark brown hairs, which are directed distad and extend to tips of fingers. There is a prolongation of these dark brown hairs proximad along the postaxial side of forearm for about 10 mm.

b. *Vibrissae (text fig. 6).*

Of the three possible vibrissal groups of the forelimb only one, the ulnar carpal, is developed and has but one papilla and vibrissa. Papilla well developed, being raised about 0.5 mm. above surface of surrounding skin, and being about 1 mm. across at its base. Vibrissa poorly developed, being of same colour and about same length (15 mm.) as surrounding hairs of forelimb.

In palmar view of hand, the papilla of ulnar-carpal vibrissa is seen just on post-axial side of axis of forelimb and about 15 mm. from proximal end of hypothenar pad of manus; i.e. with the animal orientated as in pl. I, the papilla is on inner caudal margin of forelimb.

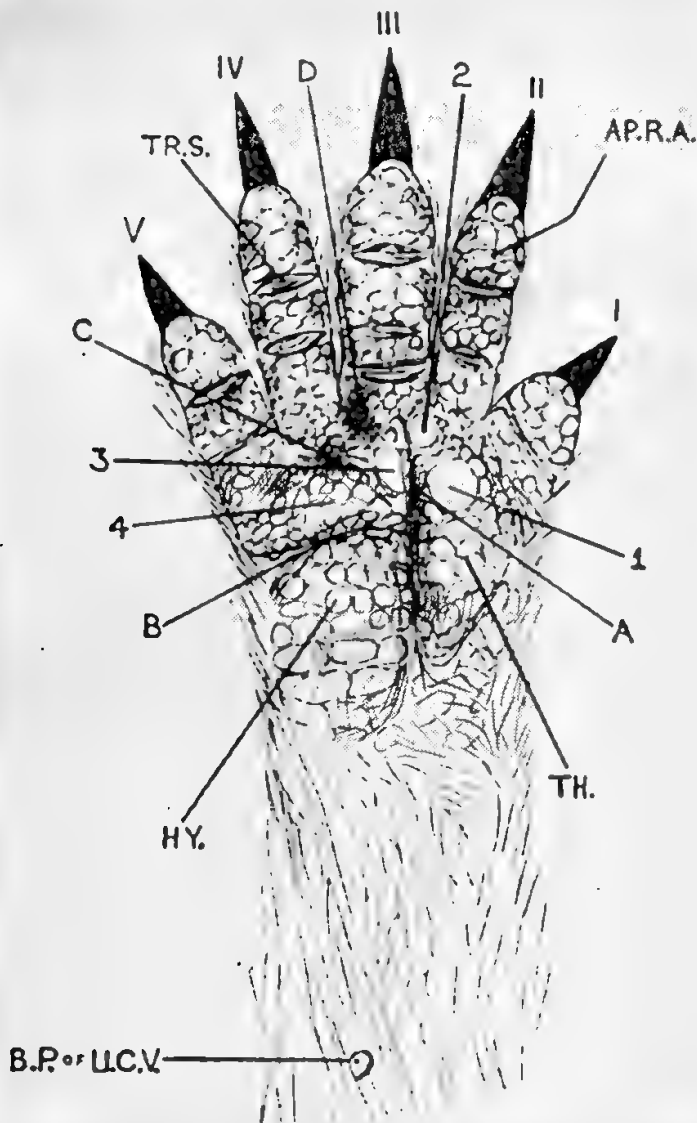
c. *Hand (text figs. 6 and 7).*

Hand has five digits, each tipped with a dark brown claw. Digital formula is $3 > 4 > 2 > 5 > 1$.

Claws all sharp-pointed, and, when viewed from the side, are

of crescentic outline (text fig. 7a). They are shorter and broader than those of a specimen of *Bettongia penicillata* which I have examined.

Third finger longer than its claw (see Tables I, III and V); other fingers are also longer than their claws, whereas in the specimen of *B. penicillata* the third finger is shorter than its claw. Apart from differences in size between the claws of *S. brachyurus* and *B. penicillata*, they differ in their transverse



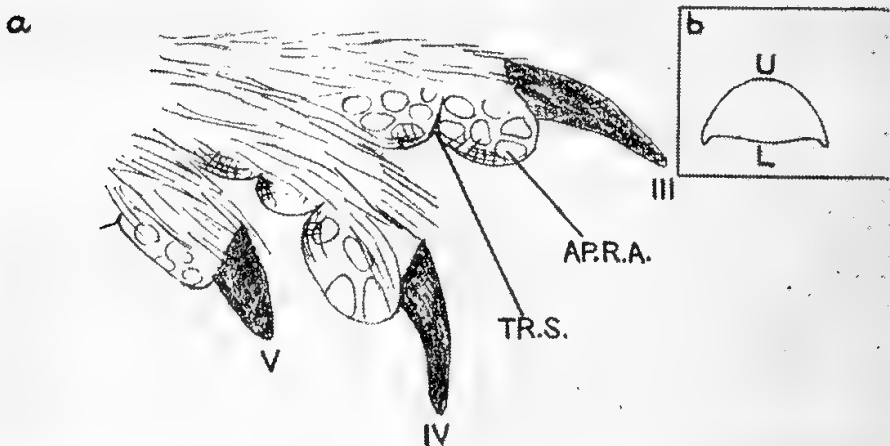
Text fig. 6.—*S. brachyurus*. Right hand, palmar surface. 2 x natural size.

I-V—fingers tipped with claws; 1-4—region of apices of 1st, 2nd, 3rd and 4th inter-digital pads. A and B—see p. 80; AP.R.A.—apical raised area; B.P. of U.C.V.—basal papilla of ulnar carpal vibrissa; C and D—see p. 80; HY.—hypothenar pad; TH.—thenar pad; TR.S.—transverse sulcus (depressed area of finger).

sections: in *Setonix* the claws have a convex upper and a plane, or slightly concave lower surface (text fig. 7b); in *B. penicillata* the claws are almost cylindrical in section, the upper surface being strongly convex, the lower surface, while not as convex, is certainly not plane or concave.

It is of interest to note that, in the specimen of *B. penicillata* examined, the skin of the palms, and the claws tipping the fingers, are of a dirty white colour. The palmar surface of the hand of *Setonix* is hairless. Its skin, which, like the claws is of a dark, dirty brown colour (cf. *B. penicillata*), is granulated. Unlike the granules on the palm of *Trichosurus vulpecula* (Wood Jones, 1924a, p. 197), the granules of *Setonix* are not arranged in lines and so do not give the palm a striated appearance.

Four sulci differentiate the palmar surface into a number of pads. The most extensive of these sulci (marked A in text fig. 6) is almost continuous with long axis of third finger. It runs from proximal to distal end of palm, turning slightly to the pre-axial side a few millimetres before it terminates between second and third fingers; it loses its definition slightly towards distal end. From post-axial margin of manus, at base of fifth finger, a sulcus (B in text fig. 6) extends transversely across palm to the longitudinal sulcus (A). From between the fourth and fifth and the third and fourth fingers, smaller sulci, (C and D in text fig. 6) run obliquely across palm towards longitudinal sulcus, losing their definition as they approach it. By references to these sulci, pads on the palm, which may be representatives of the typical palmar pads mentioned by Wood Jones (1923,



Text fig. 7a.—*S. brachyurus*. Lateral (post axial) view of fingers III-V of right hand. 2 x natural size.
Abbreviations—see text fig. 6.

Text fig. 7b.—*S. brachyurus*. Outline of transverse section through through base of claw of 3rd finger. About $2\frac{1}{2}$ x natural size.
U.—upper (convex) surface of claw; L.—lower palmar (concave) surface of claw.

p. 8), can be described. In proximal post-axial half of palm is the well developed hypothenar pad, which is bounded on its pre-axial margin by proximal part of longitudinal sulcus.

Between sulci C and B, marking distal end of hypothenar pad, is a raised area which may be interdigital pad 4. Between C and D is a second raised area which may be interdigital pad 3. Occupying the whole preaxial margin of palm is a long, raised area, the proximal half to two-thirds of which is probably made up of thenar pad; the rest is probably formed of coalesced first and second interdigital pads.

Granules of palm appear to be small and strongly differentiated in the sulci. Towards apex of each palmar pad the granules are larger, but have not such definite outlines as those within, and on the margins, of the sulci.

In addition, towards proximal end of thenar and hypothenar pads, the granules, as they approach the general undifferentiated epidermis of forearm are larger, but poorly defined. On the long raised area of pre-axial side of palm of an adult female and near base of its first finger, was an area of smooth skin about 2 mm. square. From its position it may represent the true position of the first interdigital pad. A second slightly smaller smooth area lay at base of cleft between second and third fingers—this may mark the true position of the apex of the second interdigital pad. A third smooth area of about the same size as the second occurred on longitudinal axis of manus, at base of third finger but proximal to the second smooth area. It may be the true position of the apex of third interdigital pad.

Alternatively, however, these three smooth areas may merely be parts of the palm which, in this particular animal, were subject to considerable wear and where the outlines of granules have been completely lost. However, on the distinctly granular hand of the larger and more advanced of the two pouch embryos, particularly large granules occurred, one near the base of second finger, another at base of the third, and another near base of cleft between second and third fingers. These appeared to correspond in position to the smooth areas occurring on palm of adult female just described.

Lower surface of fingers hairless and covered with the same dirty, dark brown granulated skin as palm. No distinct apical pads, but transverse sulci, corresponding to the joints between adjacent phalanges, divide each finger into raised and depressed areas, the raised being larger than the depressed and corresponding to each phalanx of a finger. Thus an apparent apical pad is produced at the end of each finger, but it does not seem to be the same as a true apical pad.

4. *Hairs of dorsal surface of abdomen.*

Hairs of dorsal aspect of abdomen, caudal to rufous area of shoulders, annulated. They vary considerably in length, ranging from

28 to 40 millimetres; proximal three-fifths of each hair dark grey, succeeded by a pale yellow or pale rufous band one-fifth of length of hair; rest of hair dark brown. Mixed with these annulated hairs are a few long (45 mm.) uniformly dark brown (black) hairs. They are confined to dorsal surface of body and do not occur on lateral surfaces, nor on limbs.

Though mixed with dark brown and rufous colours, the dominant colour of back, caudal to the rufous area of shoulder, is dark grizzled grey.

Within an arc with radius of 40 mm. of base of tail on dorsal and ventral surfaces of body, and also on dorsal (superior) and ventral (inferior) surfaces of the first 30 mm. of tail, the hair is slightly differentiated from the surrounding fur: owing to each of the three bands of colour on each hair being lighter in shade than the corresponding bands of hairs covering caudal dorsal surface of body, the hairs of this small area are, as a whole, of a lighter shade: in addition they are slightly curled.

5. *Hind limb.*

a. Hair.

Hairs of thigh and leg annulated in the same proportions and colours as those of dorsal abdominal surface.

b. Vibrissae.

No trace of typical mammalian calcaneal set for hind limb could be found in *Setonix*.

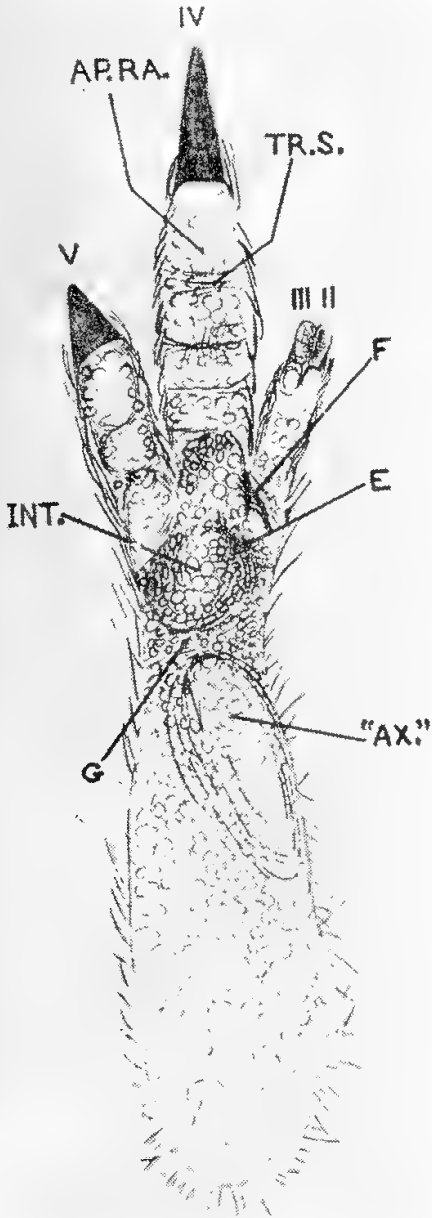
c. Foot (text figs. 8 and 9).

Foot not long and slender as in *B. penicillata*, but relatively shorter and broader. Four toes, the second and third being bound together to form a syndactylous toe. Hallux missing.

Digital formula is $4 > 5 > \widetilde{3.2}$.

Each toe is tipped with a dark brown claw. Hairs which cover dorsal surface of foot directed distad and extend to a point about 5mm. from base of claw. Because of their length they cover the tip of each toe and proximal part of each claw. They appear to be coarser than hairs covering leg and thigh. Hairs of margins of foot on the preaxial side as far as tip of syndactylous toe, and on the post axial side to base of fifth toe, uniformly grey and not annulated. Rest of dorsal surface of foot covered with dark brown hairs, which are also individually of uniform colour and not annulated. Plantar surface of foot hairless and marginal hairs of dorsal surface show no tendency to encroach on it; this contrasts with *B. penicillata* and, to a lesser extent, with *M. eugenii*, which show encroachment on the plantar surface of fourth and fifth toes and of base of the syndactylous and fifth toes.

Fourth toe, forming axis of foot, slightly less than one-third the length of foot. There is apparently no significant difference between the ratio, length of foot: length of fourth toe in *S. brachyurus* and *M. eugenii*; in the former the mean of this



Text fig. 8.—*S. brachyurus*. Plantar surface of right foot. Natural size.

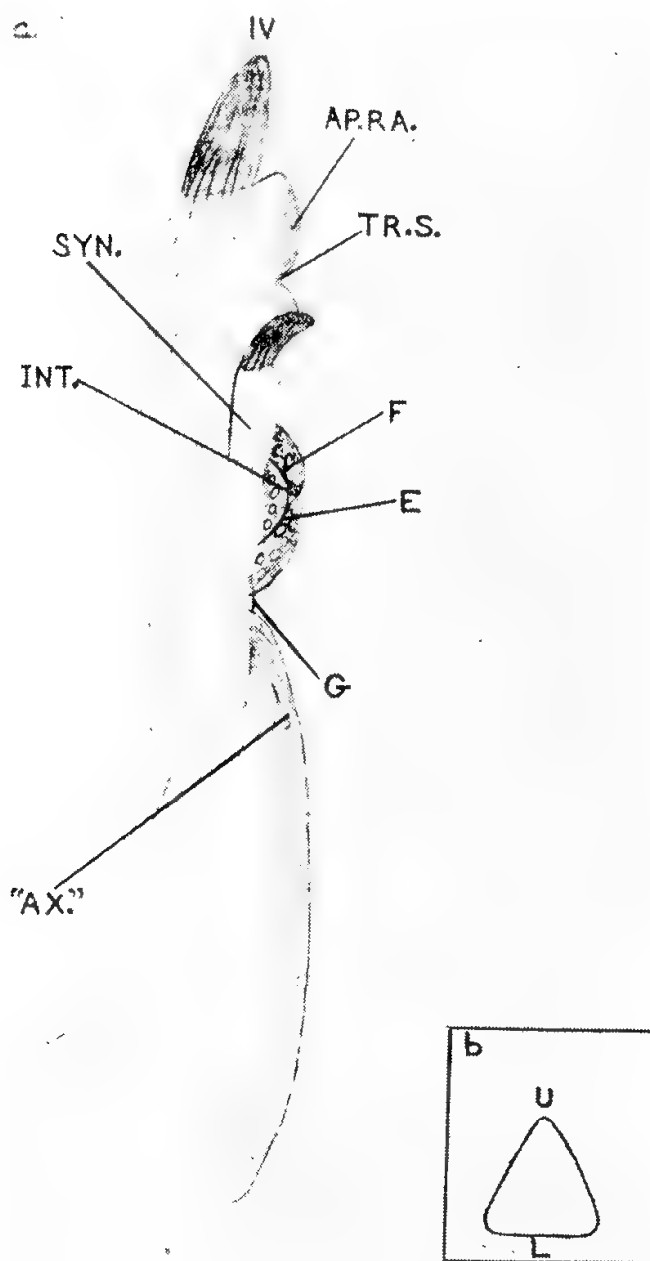
II-V—toes tipped with claws; AP.-RA.—apical (distal) raised area; "AX."—"axial pad"; E and F—see p. 85; G—see p. 85 INT.—interdigital pad; TR.S.—transverse sulcus; W.A.—worn area (post axial) over which granules lose definiteness of outline.

ratio for six animals was 1:0.32, and in the single specimen of *M. eugenii*, was 1:0.31. Finlayson (1932, p. 156) in describing the pes of *Caloprymnus campestris*, states that the ratio of pes to fourth toe is 1:0.46, which he considers much higher than that shown by the Macropodinae. It seems then that *S. brachyurus* and *M. eugenii* may be typical of their sub-family in this respect.

Claw, which is short and pointed, is about half the length of fourth toe and is deep and broad at its proximal end where it joins the toe. It is triangular in transverse section (text fig. 9b), apex of triangle being uppermost.

Fifth toe is about half as long as fourth; its claw has the same shape as, but is slightly smaller than, that of the fourth.

Syndactylous toe bifurcates 2 or 3 mm. from its distal end. Each ramus of this bifurcation is tipped by a claw of shape very different from that of fourth or fifth toes, and is directed forward (text fig. 9a). This contrasts with *Caloprymnus campestris* in which each claw of the syndactylous toes is directed



Text fig. 9a.—*S. brachyurus*. Lateral (pre-axial) view of left foot. Natural size.

SYN.—syndactylous toe. Other abbreviations—see text fig. 8.

Text fig. 9b.—*S. brachyurus*. Outline of transverse section through base of claw of 4th toe. About $2\frac{1}{2}$ x natural size.

U—upper (dorsal) surface of claw; L—lower (planar) surface of claw.

upwards (Finlayson, 1932, p. 157 and fig. 3D). Each of these claws in *Setonix* is of the same shape, and, when viewed from the side, is of crescentic outline and has a convex dorsal and concave plantar surface. Convexity of second claw faces the preaxial, that of third faces the postaxial margin of foot; the concavities of plantar side face each other and consequently that of the second claw faces the postaxial, that of the third faces the preaxial side of foot.

Skin of plantar surface dark brown (as are the claws) and granular. Granules, which, like those of palm, are not arranged in lines, are usually 1 to 2 mm. in diameter. However, in certain regions, they are transversely elongated.

A single large interdigital pad on plantar surface. It is about 20 mm. long and extends from a point about 10 mm. proximal to base of fourth toe, to a point about 10 mm. along the latter. It occupies almost the full width of foot at base of toes. At proximal end of interdigital pad, and dividing plantar surface into proximal and distal portions, is a transverse depression (G in text figs. 8 and 9), 3 to 4 mm. across and widening considerably as it nears the preaxial margin of foot. Distal part of foot includes toes and interdigital pad; proximal part has a rather wide, plane surface, with granules of varying size and definition.

Granules at apex of interdigital pad enlarged, but have not such well defined outlines as granules of depressed areas of plantar surface, which are subject to less wear.

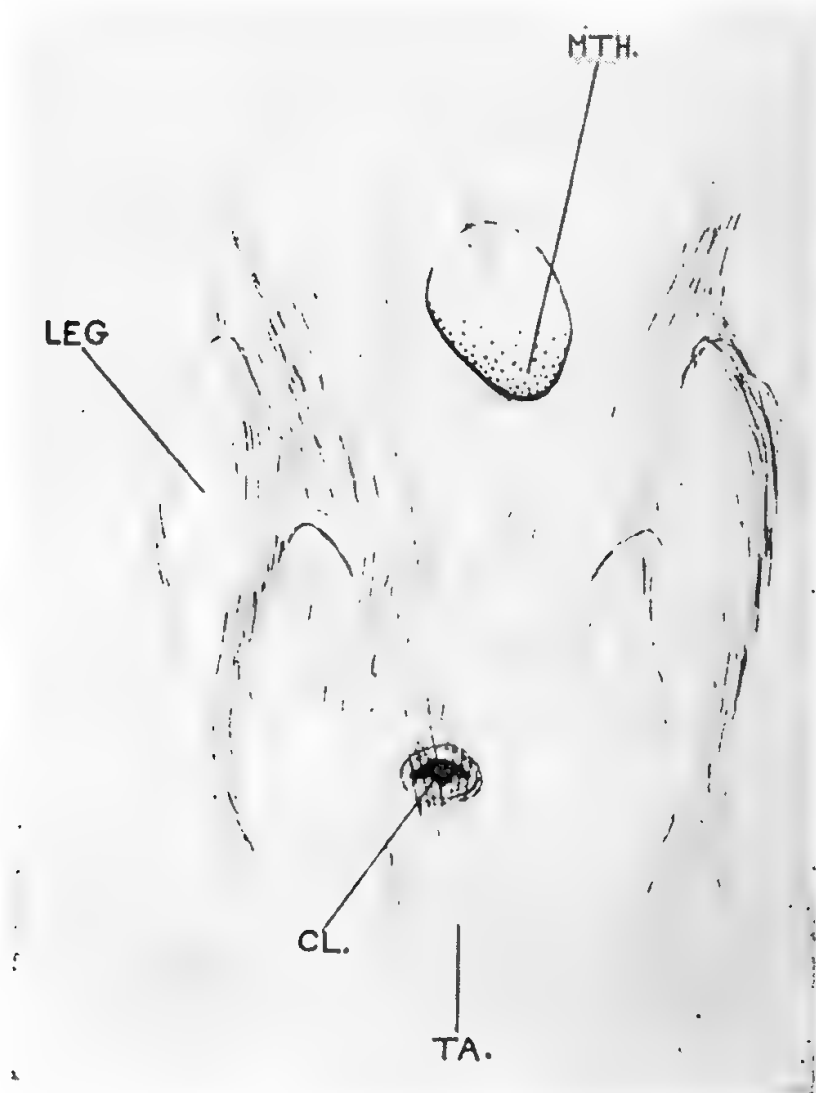
Two poorly developed sulci occur on interdigital pad. One, marked E in text figs. 8 and 9, is about 5 mm. long, rather shallow and wide, and runs from proximal and preaxial margin of pad obliquely across it towards cleft between fourth and fifth toes. The second, F in text figs. 8 and 9, is even more poorly developed, and extends from a point adjacent to cleft between the syndactylous and fourth toes, back towards distal end of E but fades out before reaching E. There are well developed creases between interdigital pad and bases of syndactylous, fourth, and fifth toes.

As with fingers, there are transverse sulci, corresponding to joints between adjacent phalanges, on the fourth and fifth toes which divide each toe into a number of relatively extensive raised and small depressed areas, each raised area corresponding to a phalanx. Distal raised areas of fourth and fifth toes have their granules transversely enlarged and flattened, the dimensions of the granules being 3 x 1 mm. Areas do not look like true apical pads.

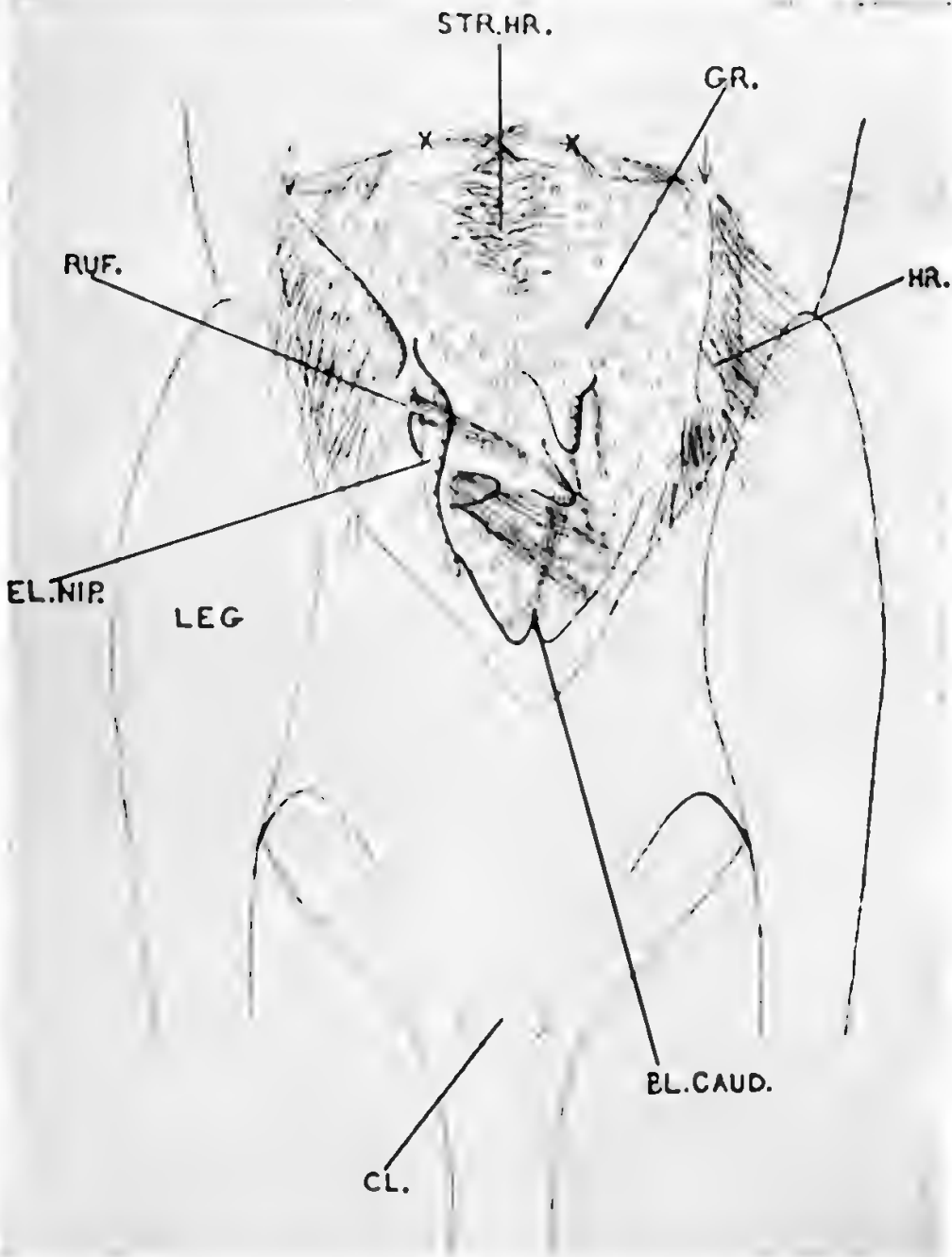
Syndactylous toe plays little part in locomotion. Skin on its plantar surface therefore soft, its granules poorly developed. It has no well defined, deep transverse sulci like those of fourth and fifth toes. On proximal division of foot there seems to be a

rather ill defined raised area (an "axial pad") running obliquely across its surface from middle line at the transverse depression, to preaxial margin of foot, about 40 mm. from its proximal end. Granules on this "axial pad" well defined, circular, and up to 2 m. in diameter. From it, towards the postaxial margin and proximal end of foot, the granules enlarge but lose definiteness of outline. Thus, on preaxial half of this proximal division, there is a raised area with well defined granules, and on post-axial half, extending towards the preaxial side at the proximal end of foot, is a flat area where the granules tend to be transversely enlarged, but are ill defined. This pattern of the proximal part of plantar surface suggests uneven wear and therefore an uneven gait. Careful examination of the "tracks" of the quokka might test this suggestion.

Granules covering proximal plantar surface of foot of *M. eugenii* did not show signs of this supposedly irregular wear.



Text fig. 10.—*S. brachyurus*. Ventral surface of caudal part of abdomen of female. $\frac{1}{2}$ natural size.
CL.—external opening of cloaca; MTH.—mouth of pouch; TA.—base of tail.



Text fig. 11.—*S. brachyurus*. Ventral surface of caudal part of abdomen of female. Pouch opened up by mid-longitudinal incision of its ventral wall and its lateral and ventral walls laid aside. All hair of surrounding ventral abdominal wall omitted. Natural size.

X-X—mouth of pouch; between arrows—maximum width; **BL. CAUD.**—blind caudal end of pouch; **CL.**—external opening of cloaca; **EL.NIP.**—elongate right cephalic nipple (see p. 83); **GR.**—granular inner surface of pouch; **HR.**—rufous hair of ventral and lateral inner wall of pouch; **RUF.**—long rufous hairs arising from base of nipple; **STR.HR.**—strip of hair extending short way down mid-dorsal inner wall of pouch; **TA.**—base of tail.

6. *Hair of ventral surfaces of abdomen.*

Apart from two specialized areas round opening of pouch in female, and round and on scrotum in male, the ventral aspect of the body, including the inner surfaces of limbs, is of a silver grey colour which becomes a grizzly grey on flanks. Hairs become longer from neck towards tail, reaching a maximum of up to 35 mm. in pubic region. Each hair dark grey for its proximal two-thirds, changing to silver grey in distal third.

7. *Pouch* (text figs. 10 and 11).

Pouch situated on ventral surface of abdomen, between caudal end of thorax and the cloacal orifice. Its mouth, directed forwards, is surrounded by dark rufous hairs. It is roughly triangular in shape, though this, and its size, can probably be changed by muscular action. Pouch of one specimen, which contained the smaller poorly developed pouch embryo, had a mouth whose transverse diameter was 14 mm. the other diameter being 10 mm. In another specimen, which had no embryo, the corresponding measurements were 35 mm. and 24 mm. It may be, then, that when a young pouch embryo is present, the size of the mouth is reduced affording greater protection for the young animal. When empty, or when the pouch young is becoming independent of its parent, the mouth is possibly relaxed and larger.

In an area about 5 mm. wide round pouch opening, the hairs, each of which has a marked uniform rufous colour, are shorter and sparser than elsewhere on ventral surface. Thus pouch opening with its fringe of rufous hairs, is in marked contrast to the rest of ventral surface of body.

Pouch cavity is of maximum width just within the mouth. In one animal, the pouch of which was 60 mm. long, this maximum width was 45 mm. It tapers gradually to a blind caudal end.

Four nipples occur on inner dorsal surface of pouch, and they may be designated right and left cephalic, and right and left caudal nipples. Cephalic pair about 35 mm. from mouth of pouch. There is a space of about 15 mm. between the pairs and about 5 mm. between the cephalic and caudal nipples on each side; thus the four are comprised within an area of about 15 x 5 mm.

In the specimen with the smaller pouch embryo, the right cephalic nipple, to which the embryo was attached, was about 20 mm. long, the left cephalic was 10 mm., and the two caudal were 5 mm. long. Thus, when in use a nipple is a greatly elongated cone fitting far into mouth of embryo: those which are not in use are considerably shorter cones.

Inner surface of pouch has an uneven covering of rufous, silky hairs, the longest of which (up to 33 mm.) arise in clusters from base of each nipple. A strip covered with rufous hairs extends from the mouth for about 15 mm. down mid dorsal inner surface of pouch. Ventral inner wall of pouch fairly well covered with rufous hairs up to 15 mm. in length, but caudal wall has a very sparse covering of rufous hairs.

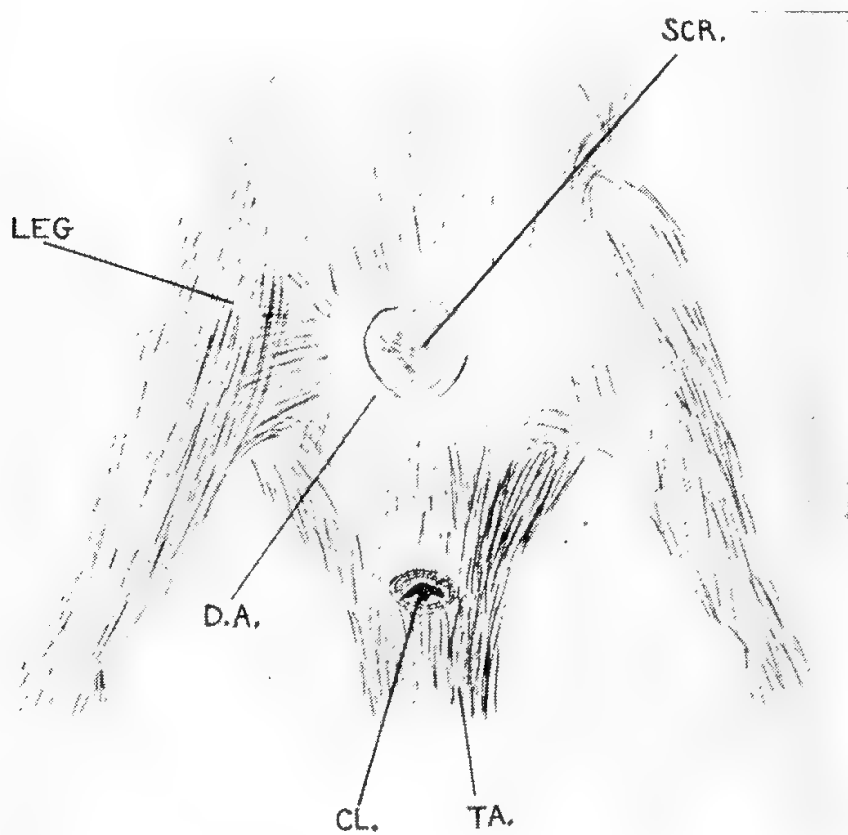
Skin lining pouch dirty white in colour and irregularly folded. These

fold, largely longitudinal, may have been the result of preservation. Skin distinctly granular, the granules of internal dorsal surface being circular and about 1 mm. in diameter. Towards edge of dorsal wall and on lateral and ventral walls, they lose their definition.

18. *Scrotum* (text figs. 12 and 13).

Owing to a very complete descent of the testes the scrotum is conspicuous and pendulous. Its dorsal (superior) surface is about 4 mm. below the ventral abdominal wall and supported by a neck or pedicle about 15 mm. wide and 5 mm. thick from front to back. Neck arises from a depression on ventral abdominal wall, which is about 5 mm. deep, 17 mm. wide (transverse) and 8 mm. long (cephalo-caudal). Surrounding this depression, and therefore surrounding junction of neck with ventral body wall, is a circular area, about 30 mm. in diameter, which, being covered by very fine, silky, pale yellow or white hairs, contrasts markedly with surrounding abdominal surface. Although, in several preserved specimens, the hair covering scrotum was light grey, in a living male it was rufous or brown and contrasts with the silver grey of ventral surface of body.

Hairs of scrotum most abundant on ventral (inferior) surface and become sparser towards dorsal surface and pedicle. Dark grey pigment



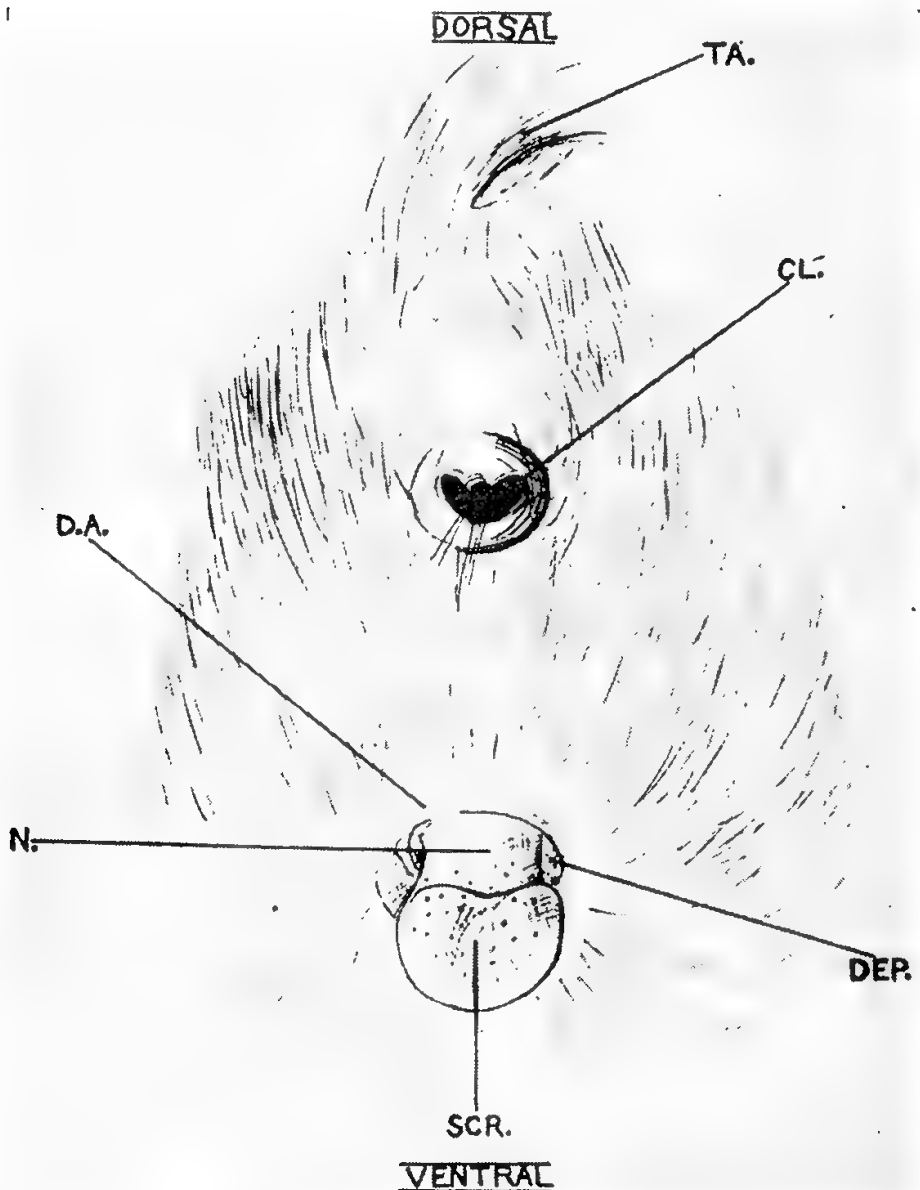
Text fig. 12.—*S. brachyurus*. Ventral surface of caudal part of abdomen of male. $\frac{1}{2}$ natural size.

CL.—external opening of cloaca; D.A.—differentiated area around junction of neck of scrotum with ventral body wall; SCR—scrotum; TA—base of tail.

spots, less than 0.5 mm. across, occur on skin of scrotum, but are more apparent, and perhaps more numerous, on dorsal surface, where the covering of hair is thinner.

When viewed from ventral or from caudal aspects the scrotum is seen to be heart-shaped. It is from 20 to 25 mm. in cephalo-caudal length, from 15 to 20 mm. in transverse width and is about 15 mm. deep (i.e. from dorsal to ventral surfaces).

There is a depression, marking outline of testes, in the mid-cephalic, ventral, and caudal surfaces of scrotum.

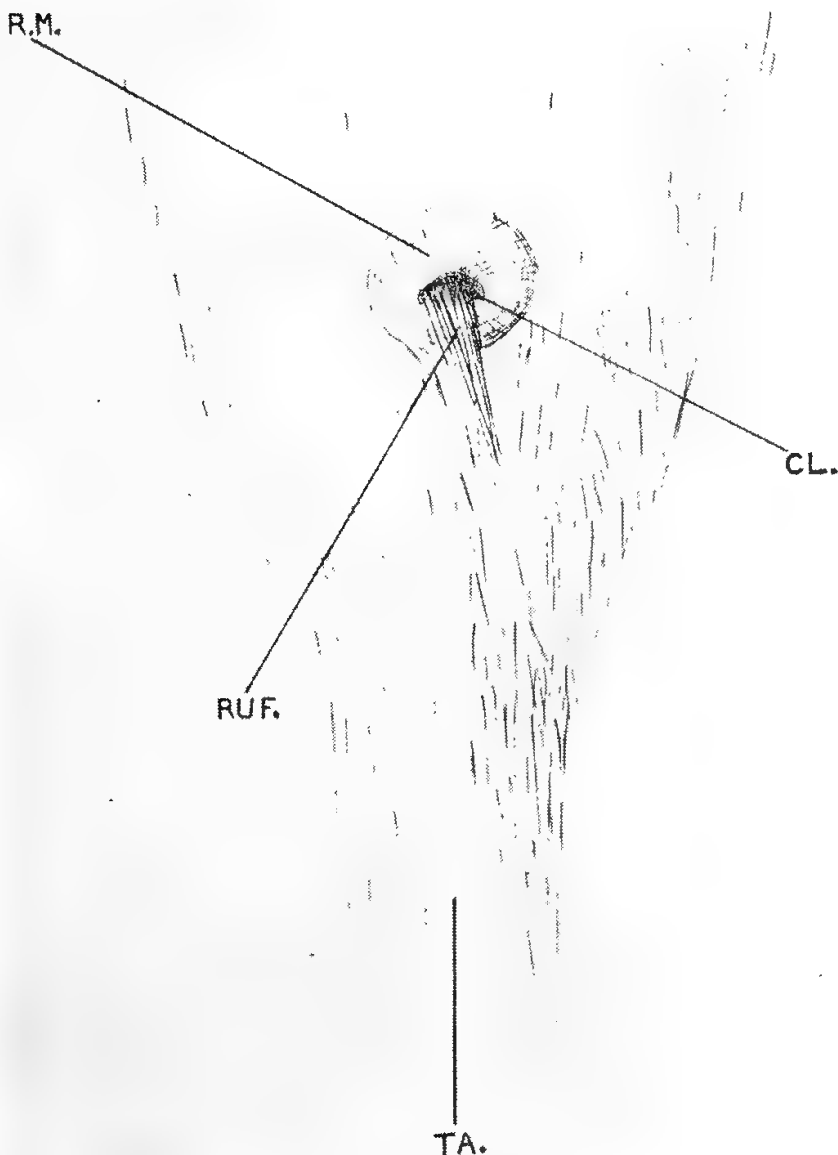


Text fig. 13.—*S. brachyurus*. Caudal view of scrotal and cloacal regions. Hair covering scrotum omitted, but skin shown with a few pigment spots. Natural size.

N.—neck (pedicle) of scrotum; DEP.—depression around base of neck where it joins ventral abdominal wall. Other abbreviations see text fig. 12.

9. *External opening of cloaca* (text figs. 13 and 14).

Margin of opening of cloaca, raised to form a flat-topped, circular ridge, sparsely covered with hairs, grey and about 5 mm. long on outer side of ridge, but becoming rufous and longer towards opening of cloaca. In both sexes on the inner (cloacal) side of ridge, almost from within cloaca itself, arise a number of long (20 mm.) rufous hairs. These may be cloacal vibrissae, described by Wood Jones (1920, p. 366) as occurring in pouch specimens and adults of *Trichosurus vulpecula*.



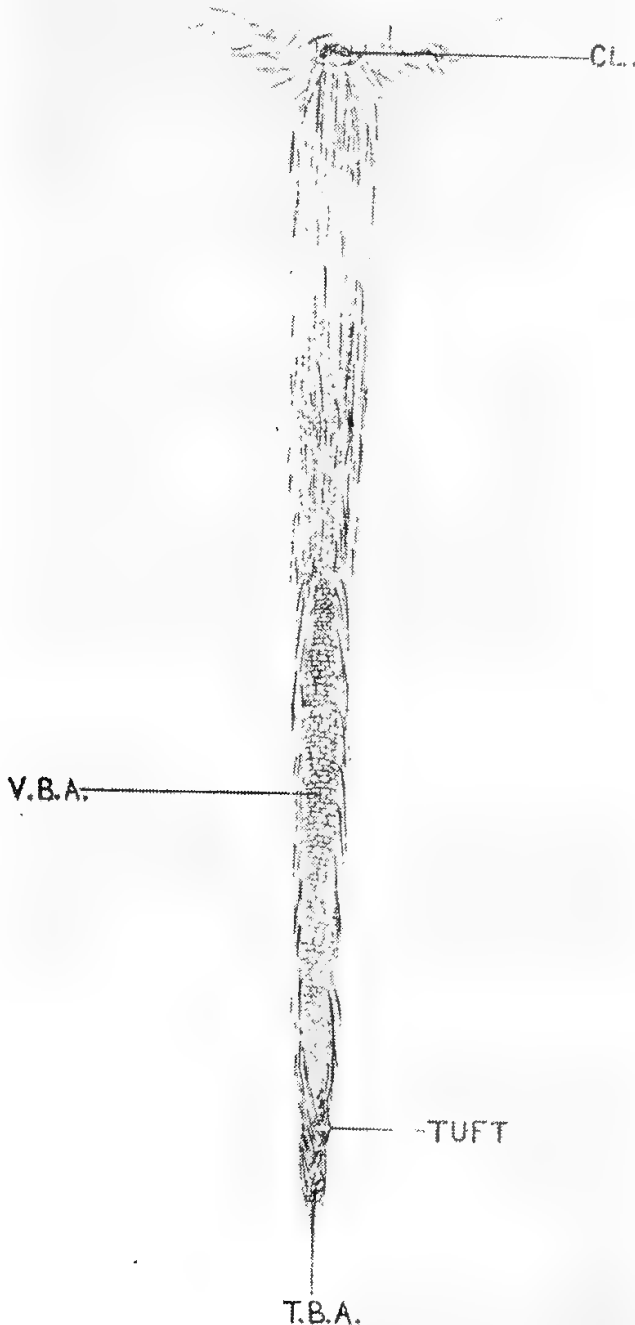
Text fig. 14.—*S. brachyurus*. Region of external opening of cloaca. Natural size

CL.—external opening of cloaca; R.M.—raised margins of cloaca (see p. 91); RUF.—long rufous hairs arising almost from within cloaca; TA.—base of tail.

10. Tail (text figs. 15 and 16).

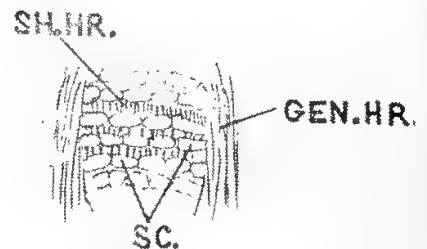
The fact that the tail of *Setonix* is short has been mentioned on p. 60 of the "Introduction" and on pp. 71 and 73 of the "Examination of Measurements," where it is suggested as being relatively shorter than that of *M. eugenii*.

Except for its first 40 mm. (see p. 82 of "Externals"), tail sparsely covered with short hairs, which are directed toward its tip and the scaly skin of tail becomes very obvious. Hairs of dorsal (superior) surface of tail banded. Proximal and distal bands brown, middle one pale rufous. Hair of lateral surfaces of tail grey and on ventral (inferior) surface silver grey or white, in conformity with general silver grey colour of ventral surface of body.



Text fig. 15—*S. brachyurus*.
Ventral (inferior) surface of
tail showing scaly epidermis.
 $\frac{1}{2}$ natural size.

CL.—external opening of
cloaca; T.B.A. — terminal
bare area; V.B.A.—ventral
bare area.



Text fig. 16.—*S. brachyurus*.
Enlargement of portion of
the ventral bare area of tail
shown in fig. 15. $1\frac{1}{2}$ x na-
tural size.

GEN. HR.—general and re-
latively long hair covering
most of tail; SC.—scales of
tail; SH. HR.—short worn
hair of ventral bare area.

In adults, distal half of ventral surface of tail apparently bare. Bare area is 100 mm. or more long and extends for the full width of ventral surface of tail. Ventral bare area does not extend to tip. However, in adults a very small terminal bare area about 5 mm. long and wide is developed.

Over the ventral bare area scales of skin become even more apparent than elsewhere on tail. Close examination shows that this area carries very short hairs, less than 1 mm. long, which arise between successive scales, as do the other longer hairs of tail.

An immature male specimen showed no terminal bare area and a very small ventral one about 30 mm. long. It seems then that this area gets larger as the animal grows older.

In contrast with *Setonix*, *M. eugenii* has a tail well covered with hair and showing no trace of a ventral bare area, although *Macropus* probably drags its tail on the ground when travelling slowly, as does *Setonix*.

Finlayson (1932, p. 160) after referring to the scaly epidermis of the tail of *Caloprymnus campestris*, says ". . . the under surface of the tail retains its dense covering through life, and its condition is exactly that of the typical wallabies and kangaroos." This, together with my observations on the tail of *M. eugenii*, accentuates the peculiarity of the ventral bare area of the tail of *Setonix*.

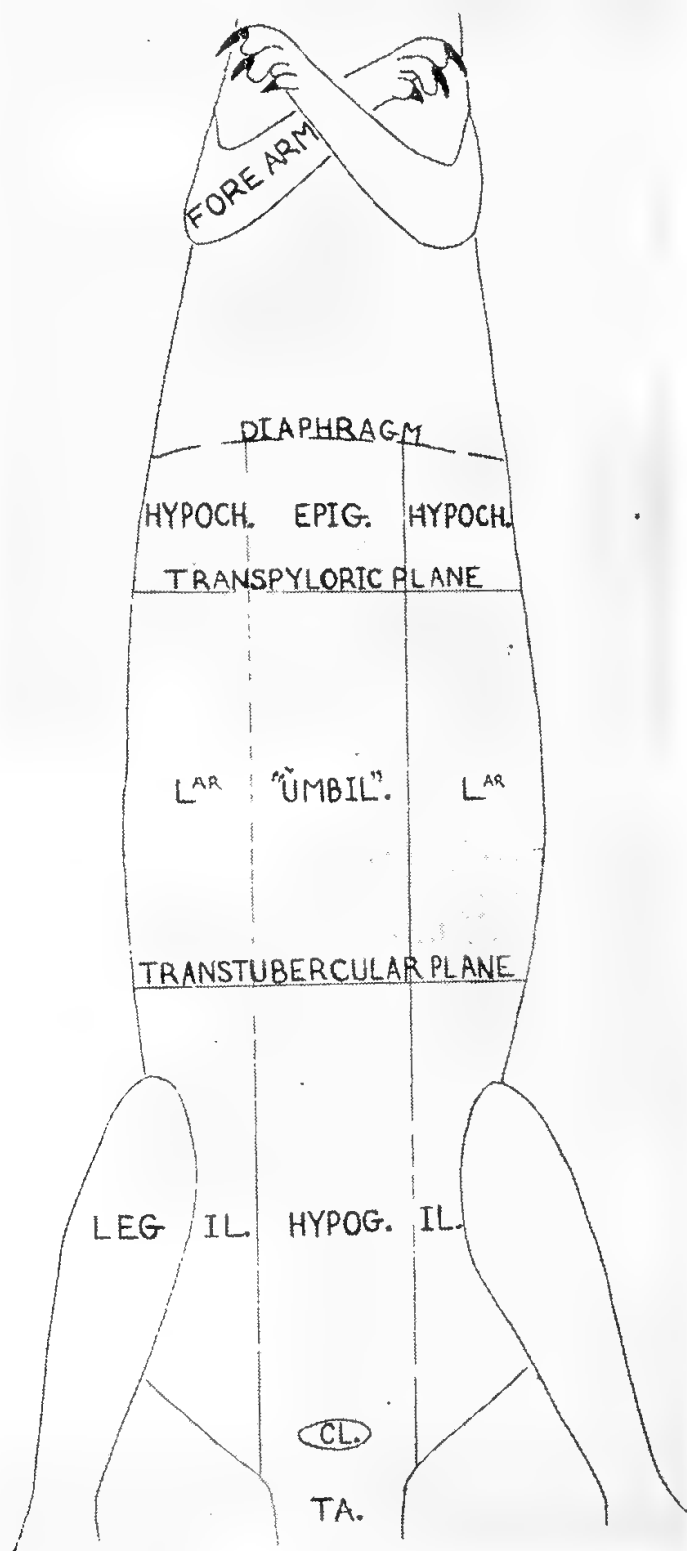
Hairs of greater part of dorsal surface of quokka's tail are up to 5 mm. long and, except for those on bare area, are shorter than those of ventral surface, which are up to 8 mm. long.

At distal end of tail the hairs of upper and lower surfaces become longer and form a small terminal tuft, the dorsal hairs contributing to which are up to 10 mm., the ventral up to 15 mm. in length.

In the immature male animal, whose ventral bare area is not very extensive, the distal 70 mm. of lower surface of tail are crested through elongation of the hairs, which are directed distad and towards middle line. In adults, owing to the development of ventral and terminal bare areas, this crest is reduced to a terminal tuft.

At proximal end, tail is flattened dorso-ventrad, so that transverse measurement (23 to 29 mm.) may exceed vertical by 5 mm. Dorso-ventral flattening is maintained for the first 40 mm; remaining distal part of tail grades from circular to laterally flattened section. Apart from the shortness of the tail, its most striking feature, noted by Waterhouse (1846, p. 162) is its scaly appearance, made more apparent by sparseness of hairy covering. Cephalo-caudal length of each scale, about 1 mm., and transverse width, about 3 mm. They are arranged in rings around tail and closely resemble those on tail of the white rat (*Mus rattus*), overlapping on all surfaces except lower, where their size and definiteness of outline is slightly reduced by wear.

Finlayson (1932, p. 160) and Gregory (1910, p. 146) mention the presence of scales on the tail of *Caloprymnus campestris* and *Petrogale* respectively.



Text fig. 17.—*S. brachyurus*. Ventral view of abdomen showing relative positions of planes dividing it up into various regions. (See Cunningham, 1937, p. 572; Gray, 1916, pp. 1068-9). About $\frac{1}{2}$ natural size.

CL.—external opening of cloaca; EPIG.—epigastric region; HYPOCH.—right and left hypochondrium; HYPOG.—hypogastric region; IL.—right and left iliac region; LAR.—right and left lumbar region. TA.—base of tail; "UMBIL."—umbilical region.

In a well advanced, hair-clad, pouch embryo (*Macropus* sp.), the skin of tail showed creases but no scales. Skin of tail of *M. eugenii* appears to be merely lined and not scaly.

Gregory (1910, p. 146) in discussing the origin of hairs in mammals, attaches some importance to "the mingling of hairs and minute scales in the foetal *Dasypus* and in the tail of *Didelphis*, *Petrogale*, and many insectivores and rodents. The tail, being of little adaptive importance in the economy of many animals might be expected to retain in some instances very ancient hereditary characters."

I wonder whether the scales on the tail of *Setonix* would have been regarded (by Gregory) as a very ancient hereditary character, like those on the tail of *Petrogale* and other mammals, or whether, as seems more reasonable, the scales would be regarded as a secondary feature of the skin. I have been unable to examine the tail of *Petrogale* and so cannot assess the resemblance or differences between the condition of its tail and that of *Setonix*.

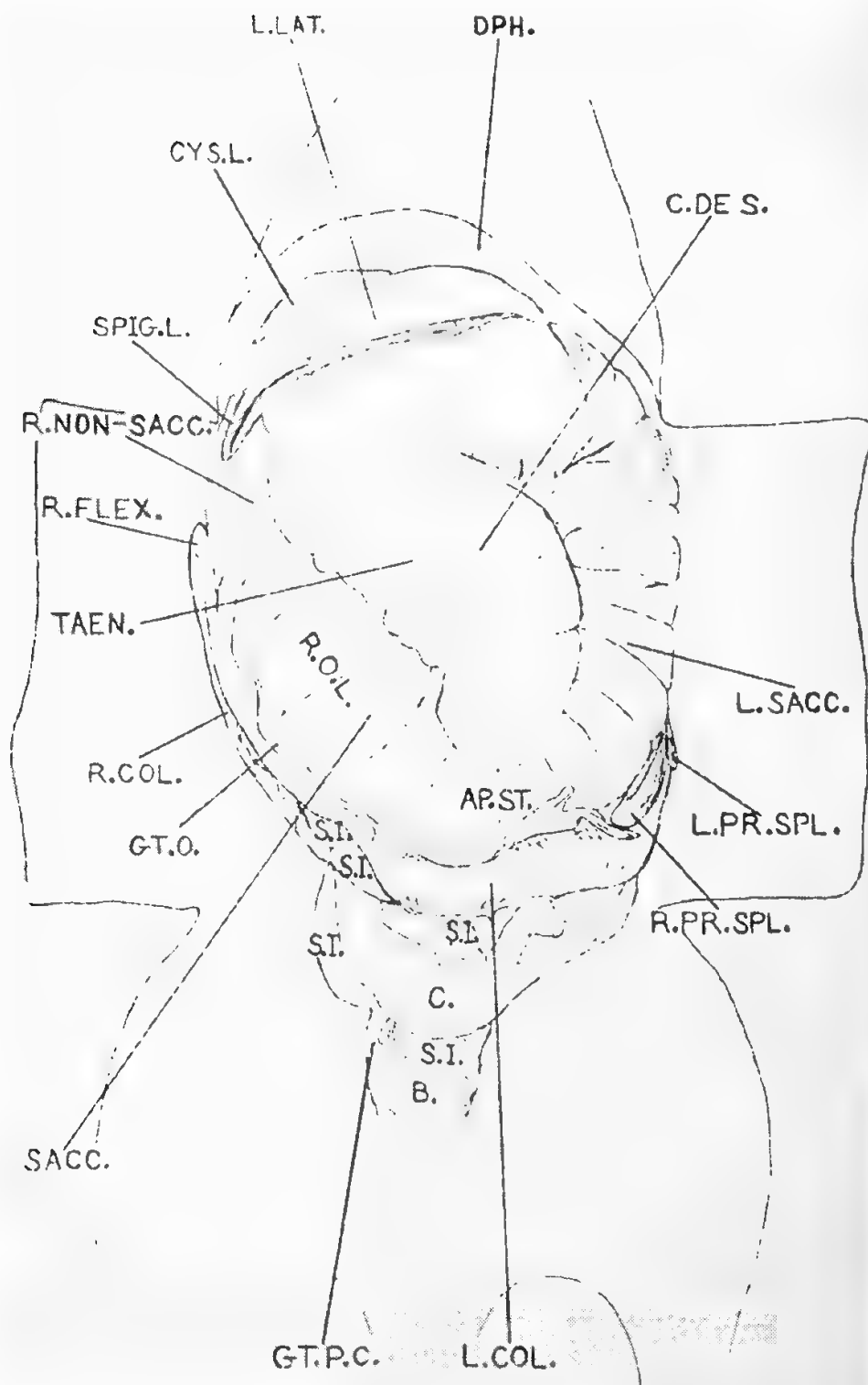
III.—LARGE INTESTINE.

A.—INTRODUCTION.

Cunningham (1937, pp. 593-4) uses the term large intestine to include caecum, colon and rectum. Mitchell appears to use the term *hind-gut* to cover colon and rectum, excluding caecum. Thus large intestine may be regarded as made up of a caecum and hind-gut.

In describing the large intestine of *Setonix* I have largely consulted Mitchell (1905, 1916), Beddard (1908), and Mackenzie (1918a and b; 1919). The descriptions of these authors is apparently based on the examination of fewer specimens of a given genus or species, than the seven of *Setonix* available to me. Mitchell and Beddard are concerned with the evolution of the pattern of the mammalian intestine, including the development of secondary loops of the colon (*ansae coli*), the formation of the cavo-duodenal and colico-duodenal ligaments and the homologies of the mammalian caecum. Beddard devotes more attention to secondary adhesions between remote portions of the intestine than does Mitchell, who concentrates more on the caecum and secondary loops of the intestine. They describe the intestinal pattern of most mammalian groups, including notes on that of macropods, other than *Setonix*.

Mackenzie (1918b) has described the gastro-intestinal tract of marsupials in detail. He devotes a section to macropods, of which he has examined a number of subgenera and species excluding *Setonix*. Unfortunately he gives no bibliographical list, so I cannot trace his terms. He either describes a completely new set of adhesions, or uses different names for those structures described by Mitchell and Beddard. The latter seems more reasonable, and accordingly I consider that his *mesial fold* is equivalent to the *colico-duodenal ligment* of Mitchell and Beddard, and his *right lateral* or *duodeno-mesocolic fold* is equivalent to their *cavo-duodenal ligment* (*ligamentum cavoduodenale*).



Text fig. 18a.—*S. brachyurus*. Ventral view of abdominal viscera *in situ*. Stomach considerably distended with food. $\frac{1}{2}$ natural size.

AP.ST.—apex of stomach; B.—cephalic end of bladder; C.—caecum; C DE S.—cul-de-sac of cardiac extremity of stomach; CYS.L.—cystic (mesial) lobe of liver; DPH.—diaphragm; GT.O.—fold of greater omentum; GT.P.C.—greater (false) pelvic cavity; L.COL.—left (distal) colon; L.LAT.—left lateral lobe of liver (note accommodation of stomach); L.PR.SPL.—left (dorsal) process of spleen; L.SACC.—left sacculated (car-

However, Beddard is uncertain about the occurrence of the colico-duodenal ligment in marsupials and it is this which has caused my doubt as to whether the mesial fold is the colico-duodenal ligament. As I have followed Mackenzie for more detailed description of peritoneal adhesions in the colico-duodenal region, I have used his term (mesial fold) in this paper.

Klaatsch (1892) has described the evolution of the pattern of the intestine from Amphibia through Reptilia to the Mammalia. Within the mammals, he describes the complications of the colon involving the formation of secondary loops, and secondary adhesions between morphologically remote portions of the intestine. He devotes two sections to the description of the intestine of marsupials with notes on that of *Halmaturus*.

The colon of *S. brachyurus* appears to be much more simple than that of other macropods. Accordingly it can be divided into distinct and straight ascending, transverse and descending parts. Klaatsch (1892, p. 662) uses these terms with reference to the colon of *Halmaturus thetidis* (*Macropus thetidis*).

B.—CAECUM AND ILEO-CAECAL REGION.

1. *Caecum* (text figs. 18a, 19-23, 25).

a. *Position in situ* (text fig. 18a).

Agreeing with what Mitchell (1916, p. 206) said of the caecum in mammals generally, in *S. brachyurus* it may be regarded as a forward continuation of hind-gut, the apex being directed parallel to ileum and towards proximal end of small intestine.

In *Setonix* the ileum and caecum meet at an angle that varies from individual to individual, but is always acute, being usually between 40° and 70°. This is in accord with what Mitchell (1905, p. 450 and fig 7) describes for *Bettongia penicillata* and infers for *Macropus bennetti*, when he says that the latter has a gut pattern essentially similar to that of *B. penicillata*; he does not specifically mention the angle between the ileum and caecum in *M. bennetti*.

From its proximal or basal end, at junction of colon and ileum in dorsal aspect of caudal part of right lumbar region, the caecum, running ventrad, usually extends obliquely to the left across the caudal portion of the abdomen. Its distal blind end is in mid-hypogastric region. The length of caecum, and consequently its right-to-left extent, varies from one specimen to another; in several specimens caecum extended no farther to

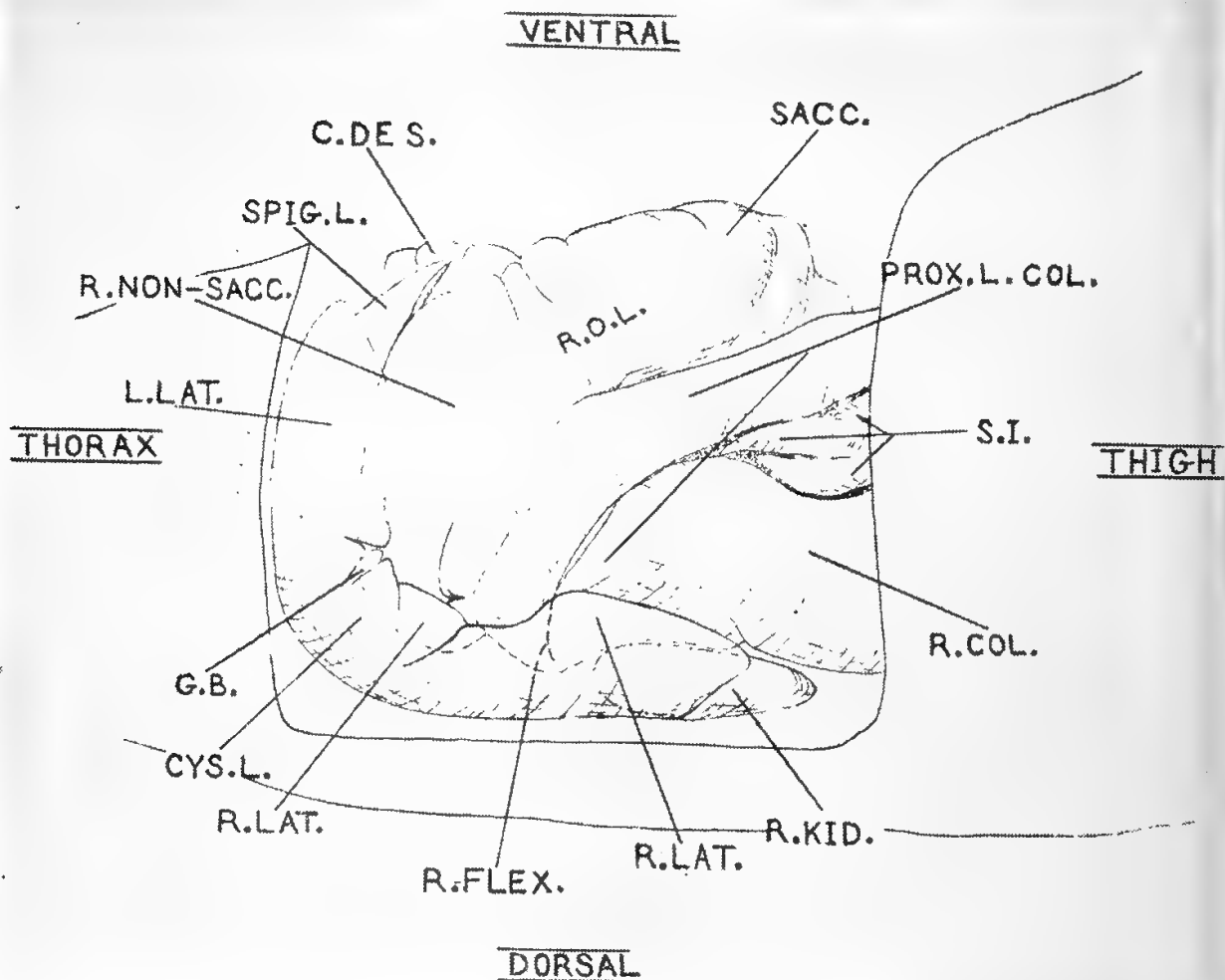
diac) portion of stomach; R.COL.—right (proximal) colon; R.FLEX.—right transpyloric or post-hypochondrial flexure of colon; R.NON-SACC.—right pyloric or non-sacculated portion of stomach; R.O.L.—right oblique limb of stomach; R.PR.SPL.—right (ventral) process of spleen; SACC.—sacculated part of right oblique limb of stomach; S.I.—small intestine; SPIG.L.—spigelian lobe of liver; TAEN.—a taenia of the stomach.

the left than the hypogastric region, whereas in one animal its distal tip lay in the left iliac region (text fig. 18a).

b. Shape and dimensions (text figs. 19–21, 23, 25).

Caecum of *Setonix* short, relatively wide, and rather blunt, maintaining a fairly constant calibre throughout its length. Length from 43 to 61 mm. and maximum circumference 60 to 85 mm.

The caecum in my specimens was not circular in section, but probably through pressure of adjacent viscera, was somewhat flattened. As the degree of flattening was about the same in all these specimens, comparisons of its width could be made (see also p. 103).



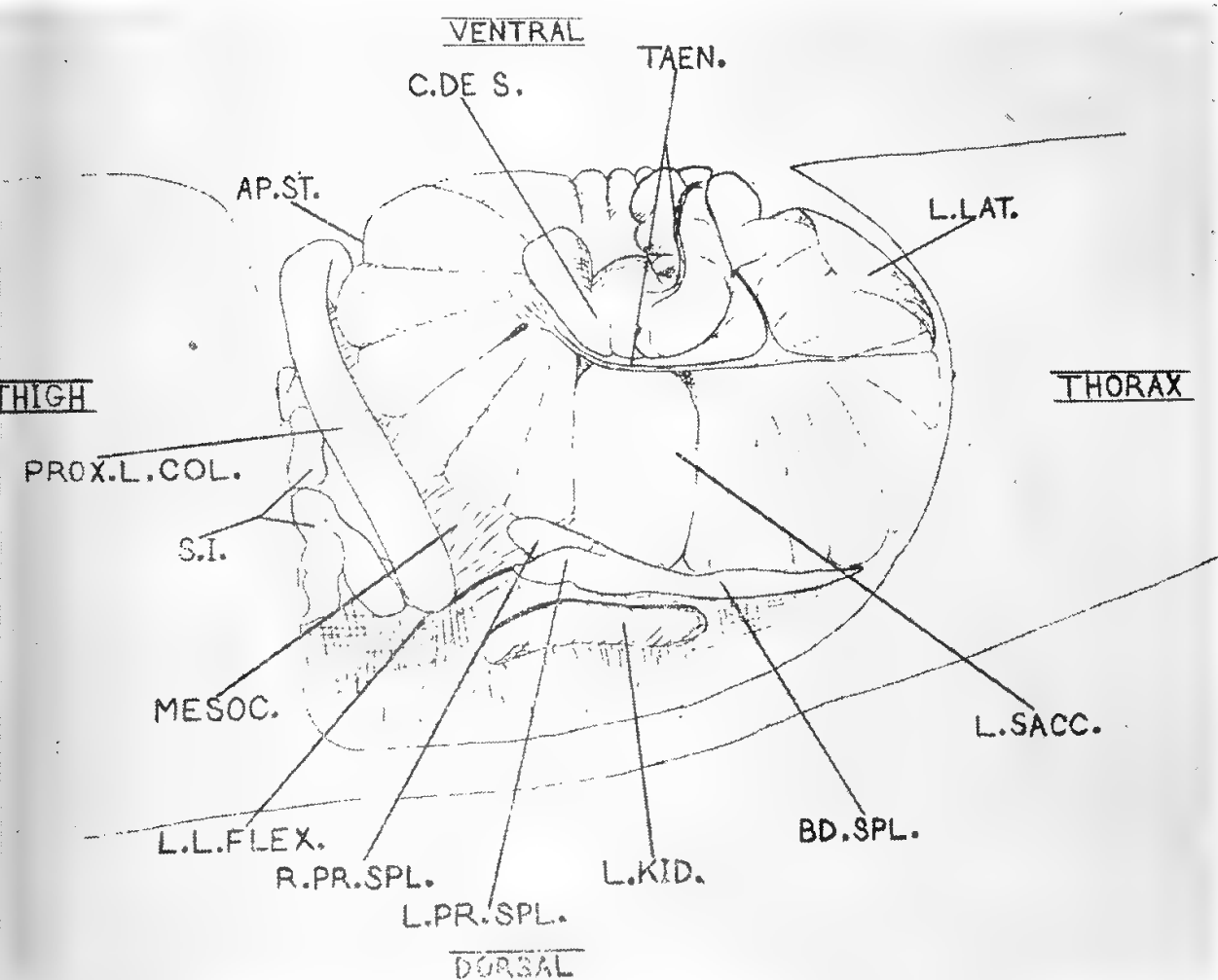
Text fig. 18b.—*S. brachyurus*. Right lateral view of anterior abdominal viscera *in situ*. (Not same specimen as is shown in text fig. 18a.) Note accommodation by lobes of liver of pyloric part of stomach, proximal part of colon and right kidney. Arrow indicates flexure of right pyloric part of stomach in right hypochondrium. Right transpyloric flexure of colon dotted in behind right lateral lobe of liver. $\frac{1}{2}$ natural size. G.B.—gall bladder; PROX.L.COL.—proximal part of left (distal) colon; R.LAT.—right lateral lobe of liver almost divided in two by fissure; R.KID.—right kidney. Other abbreviations, see text fig. 18a.

Maximum breadth about half its length. In two individuals the ratio of length to breadth of caecum was noticeably greater than 1.00 : 0.50; in the other four examined it was slightly less than 1.00 : 0.50. Probably the greater width of caecum in the two individuals was due to distention by food or to greater "flattening." Distension by food will also affect the shape, including the degree of tapering. For example, in specimen 2 the caecum, which was not greatly distended, narrowed noticeably towards its distal end. (Text fig. 19.)

c. Variations in shape (text fig. 22).

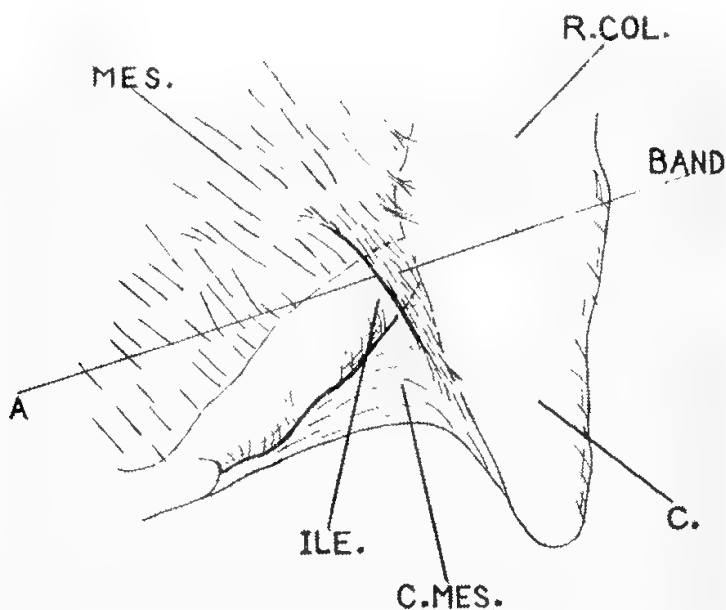
Specimen 6 showed some slight variations in the form of its caecum:—

- i. Caecum curved along its length and could not be straightened without unnatural strain on the caecal mesentery. This curvature was not found in the other specimens.



Text fig. 18c.—*S. brachyurus*. Left lateral view of anterior abdominal viscera *in situ*. Same specimen as shown in text fig. 18b. $\frac{1}{2}$ natural size.

B.SPL.—body of spleen; L.KID.—left kidney; L.L.FLEX.—left lumbar flexure of left colon; MESOC.—mesocolon of left colon. Other abbreviations, see text figs. 18a and b.



Text fig. 19.—*S. brachyurus*. Ileo-caecal region and associated peritoneal structures. Drawn from specimen 2. $\frac{1}{2}$ natural size.

A—see p. 101; BAND.—band of mesentery crossing from mesentery of small intestine to caecal mesentery; C.MES.—caecal mesentery; ILE.—ileum; MES. mesentery of small intestine and right colon. Other abbreviations, see text figs. 18a, b and c.

- ii. At proximal (basal) end of caecum there was a constriction (A, text fig. 22). Other abnormal constrictions of large intestine of specimen 6 are mentioned elsewhere in this paper (p. 102).
- d. Mesenteries associated with caecum (text figs. 19 and 21). Position of caecum relative to proximal part of right colon and distal part of ileum is to a certain extent determined by a mesentery, which has the outline of an isosceles triangle and stretches between the adjacent margins of caecum and distal part of ileum. Its extent is such that it completely fills the angle formed by the junction of caecum with distal part of ileum.

This caecal mesentery has three margins:—

- i. *Caecal*—attached to caecum, shorter than ii. or iii.
- ii. *Ileal*—attached to ileum, approximately equal to iii.
- iii. *Free*—constituting the third side of the triangle and not attached to any portion of the viscera.

Attachment of mesentery does not extend the full length of caecum but terminates 10 to 20 mm. from its blind end (cf. however, specimen 6 below). Free margin of mesentery concave. It is slightly thickened being therefore stronger than other parts of mesentery.

In specimen 6 (text fig. 22) the caecal mesentery extended to within 4 or 5 mm. of tip of caecum, instead of 10 to 20 mm. as in other specimens.

In every specimen a narrow band of mesentery crosses over the left of ileum near ileo-caecal junction; it connects mesentery of small intestine to caecal mesentery and is fused with both of them (text fig. 19). It has two margins—a free one, up to 20 mm. long (A, text fig. 19), and an attached one with adhesions to ileo-colic junction, to portions of mesentery of small intestine and to caecal mesentery. Except for these adhesions, the band of mesentery, as it crosses ileum, is quite free, and to an extent limited by this marginal adhesion to ileo-colic region, may be raised off the ileum. Width of this more mobile part of the band of mesentery (which is located about the middle of its length), may be up to 7 mm. Elsewhere along its length, the extent of the adhesion of the band to other structures, such as the mesentery of small intestine and the caecal mesentery, is increased and its mobility correspondingly decreased.

e. Conclusion on caecum.

Caecum and associated mesenteries of *S. brachyurus* do not differ markedly from the macropine condition described by Mackenzie (1918b, pp. 37-41) for other wallabies, though it is shorter and broader. Caecal mesentery of *Setonix* agrees with Mackenzie's description of that structure in wallabies, in that it does not extend to tip of caecum. However, it does not fall as far short of tip of caecum as that of the wallaby whose ileo-caecal region and associated mesentery is figured by Mackenzie (1918b, p. 38). Though no trace of the longitudinal bands described for the caecum of *Macropus major* (Mackenzie, 1918b, p. 39) could be seen on the outside of the caecum of *Setonix*, in specimen 1 (immature male) a longitudinal marking with transverse branches occurred on the inner surface directly underneath the attachment on the outside of the caecal mesentery. It was noticed after the mucosa had been scraped away. From this description it can be seen that the caecum and associated mesenteries of *Setonix* show some variation and may show slight differences from other wallabies.

2. Evidence for "caecal pouch" in adults and pouch embryos.

Mitchell notes that in *Macropus bennetti* (1905, p. 453 and fig. 8) and *Dendrolagus ursinus* (1916, pp. 197-8 and fig. 9), apart from the normal caecum, there is a "caecal pouch" also situated at the ileo-colic junction, whose position suggests that it is the remnant of the other member of originally paired caeca.

a. Examination of adults (text figs. 19-23, 25).

In adult the right (proximal) colon, which in five specimens shows no sign of constriction or sacculation, is, for greater part of its length, wider than caecum, this being particularly apparent at its proximal end in region of ileo-colic junction. Thus colon may be dilated at caeco-colic junction (text figs. 19, 20, 25). It

was thought at first that the increased calibre of the proximal part of the right colon was evidence for Mitchell's "caecal pouch," but, after comparison of the conditions in *Setonix* with Mitchell's diagrams, this idea was abandoned. In both the species examined by Mitchell the caecal pouch is shown as a very definite structure, of quite appreciable length and boundaries, which, like the normal caecum, is directed along the ileum towards the proximal end of the small intestine. The dilation in *Setonix* is much less definite; it was completely absent from one of the specimens examined and its size varied in the other five. The variation is probably correlated with the amount of food contained in that part of the intestine.

In specimen 6, a male, a strikingly different condition was found (text fig. 22). Proximal part of colon had a total of six minor constrictions on its dorsal and ventral margins, and a seventh constriction at proximal end of caecum, near its junction with colon. Most prominent of these constrictions was on ventral margin of right colon, 30 mm. distad of ileo-colic junction (G. text fig. 22). It was 4 mm. deep, and, gradually losing its definition, extended from ventral margin of colon half way up its outer (right hand aspect). There was no evidence that it extended over the corresponding portion of the left hand side of right colon. Between it and ileo-colic junction there was a sacculus, which, if regarded as a poorly developed caecal pouch, was 4 mm. long (the depth of the constriction) and 27 mm. wide (the distance between the constrictions and the ileo-colic junction).

As can be seen from these dimensions and from text fig. 22, this structure, though striking in comparison with other specimens of *Setonix* which lack it, is not as prominent as the caecal pouch figured by Mitchell.

- b. Examination of pouch embryos (for details of these see p. 61 and pp. 143-144).

Both specimens had the normal single macropine caecum. Right (proximal) colon was of uniform calibre, greater than that of ileum. As in adult, there was a slight dilation of right colon at ileo-colic junction but there was no sign of the sacculation seen in specimen 6. Thus there was no indication of a second caecal outgrowth in ileo-colic region of either pouch embryo.

- c. Conclusion.

As I have been unable to examine the viscera of either *Dendrolagus ursinus* or *Macropus bennetti* for a first-hand comparison, a definite conclusion cannot be reached as to whether or not the sacculus on the ventro-lateral margin of the right colon of specimen 6 is a rudimentary caecal pouch. Though its dimensions and shape are not convincing in this respect, its position seems to correspond with that of the caecal pouch described by Mitchell in *D. ursinus* and *M. bennetti*.

It seems that this particular sacculus, whether it does or does not

represent the second saecum of the original pair, is only exceptionally present in *Setonix*, as also are the other constrictions found on the right colon of specimen 6.

Examination of a larger number of specimens may or may not confirm this. Even if exceptional, the abnormality may be the persistence in an odd individual of an ancestral structure.

Whatever the significance of the condition of the right colon and caecum of specimen 6, it is peculiar and interesting. Rather than be evidence for a second caecum, as has been discussed here, it may represent a past or an incipient sacculation, by taeniae, of the colon.

3. *Comparative widths of ileum, caecum, and right colon in adults and pouch embryos.*

It is to be noted that, in the following brief investigation, comparisons are made between widths of the various parts of the intestine, not between circumferences. In all the animals I have examined the small intestine and right colon are flattened, so that the measurement of circumference, given in other sections of this paper, indicates better perhaps than the diameter the true calibre of sections of the intestine. Here, however, it was considered that: *Firstly*, in the adults examined, the flattening of the distal part of the ileum, caecum, and right colon was roughly the same so that comparisons of the widths of these three sections of the intestine, as indicative of relative calibres, could be fairly made. The same argument applied to the two pouch specimens in which the caecum, right colon, and distal part of the ileum were equally flattened. From the ratios of these measurements, any relative differences between pouch specimens and adults should be revealed. *Secondly*, the difficulties and possible errors involved in measurements of the circumferences of various parts of the intestine of small pouch specimens, would not justify attempting them in such a brief investigation.

a. Adults.

Maximum width of caecum about 2.5 times maximum width of distal part of ileum. Maximum width of right colon about 1.5 times maximum width of caecum.

Thus maximum width of right colon is about 3.7 times maximum width of distal part of ileum.

b. Pouch embryos.

Maximum width of caecum seems to be about equal to that of distal part of ileum in both specimens. In the older specimen, maximum width of right colon is about 1.5 times maximum width of caecum, and of ileum; in the younger, colon, caecum and ileum are of about equal calibre.

c. Conclusion.

From these facts it would appear that, as the animal gets older:—

- i. Difference in calibre between ileum and caecum increases.

- ii. Difference in calibre between ileum and right proximal colon increases.

It may be that the difference in calibre between caecum and right colon becomes marked at an earlier stage in the animal's life than i. above.

In most of the adults examined, the right colon and the caecum were distended with bulky vegetable matter, made up largely of complex polysaccharides undergoing the final stages of digestion and absorption. However, in specimen 1 (immature male) the right colon was contracted and empty (circumference 35 mm.), being of smaller calibre than the left (distal) colon (circumference 55 mm.) and not much larger in calibre than the distal part of the ileum. The caecum of this animal contained an appreciable quantity of matter, the passage of which into the right colon was probably prevented by the contraction of a caecocolic sphincter. Presumably in this animal, prior to its capture, the matter originally within the right colon had moved on to the left colon to form faecal pellets, and additional supplies of vegetable matter had not reached the right colon from the small intestine or caecum: the right colon was therefore not distended.

The pouch specimens had a diet of milk and not of bulky vegetable matter: digestion of the milk would take place before it reached the large intestine. This food would yield a very small amount of indigestible or undigested matter in the hindgut. Though some faecal material would be provided possibly by dead intestinal flora and fauna (bacteria and protozoa), there would be no cause nor use for an expanded right colon or caecum. The latter, despite the complexity of the macropod stomach (cf. ruminants), probably plays a part in the digestion of the complex polysaccharides of the vegetation on which the adult feeds, and so in adults is voluminous.

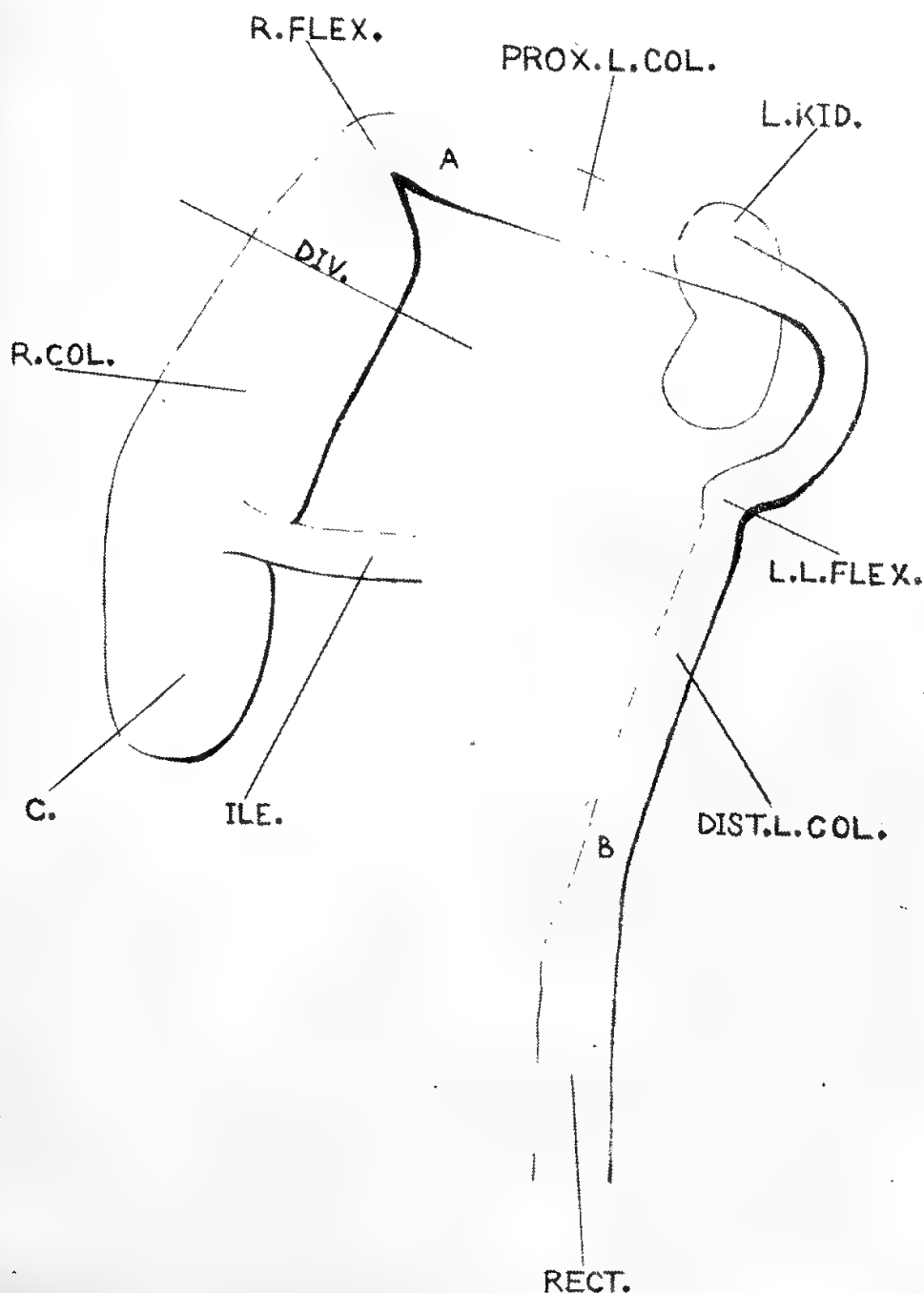
It is suggested, then, that in the adult, the calibre of the right colon and the caecum can probably vary considerably depending on the presence or absence of bulky vegetable matter. It may be that in an adult whose right colon and saecum are empty, the differences in calibre between these and the ileum might not be so apparent and the relative widths of these sections might approach more closely those in pouch specimens than do the results of my measurements. Experimental verification of the suggestion that differences in calibre between ileum, caecum, and right colon are the result of a change from a milk to a herbivorous diet, might be obtained by feeding a growing quokka on a milk diet for a longer period than the natural one: in this case differences of calibre like those mentioned above, might not be apparent. In the exceptional immature male specimen (see above) the empty right colon had walls which were much more muscular than those of the ileum. Hence it may be that, in the change from a milk to a vegetable diet, the essential change in the right colon is the development of more muscular wall, enabling considerable distension when the occasion demands.

C.—HIND-GUT.

1. Introduction.

a. Length.

Total length of hind-gut in *Setonix* is 440 to 520 mm. (cp. Beddard, 1908, p. 568). Calibre varies along its length, the



Text fig. 20.—*S. brachyurus*. Ventral view of large intestine to show its simple pattern. Left kidney shown to indicate relationship between it and left lumbar flexure of colon. All other viscera omitted. $\frac{1}{2}$ natural size.

A to B—? Ansa coli sinistra; DIST.L.COL.—distal part of left colon; RECT.—rectum. Other abbreviations, see text figs. 18, a, b and c.

maximum being in ileo-colic region. Distad there may be sudden variations in calibre due to accumulation or complete absence of faecal matter. Approximate circumferences, indicating the range in calibre for any one division of the hind-gut, are given in the descriptions of those divisions.

b. Pattern (text fig. 20).

Broadly speaking, the hind-gut of *Setonix* is Π shaped, the left arm being longer than right.

c. Divisions.

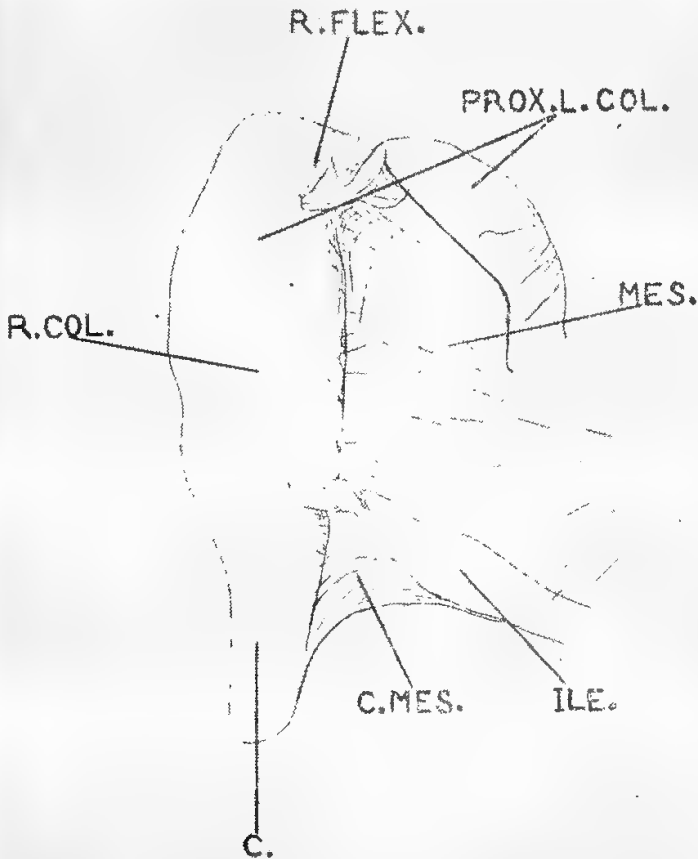
Hind-gut is divided into colon and terminal rectum. Rectum and urino-genital system joined to form a common chamber, the cloaca which opens to the exterior beneath the tail (see p. 91 of "Externals").

The colon (text figs. 18a, b and c, 20-23; 25-31) can be divided in right (proximal) and left (distal) parts. Mackenzie (1918b, p. 21) claims that this division is marked by the mesial fold, which is a sheet of peritoneum, to be described later, binding the colon to the pyloric region. Later, when dealing with the kangaroos and wallabies, he says that "The pyloric sphincter indicates the separation of the colon into two portions . . ." (1918b, p. 41).

For purposes of measurement of the various sections of colon, the pyloric constriction at distal end of sphincter, i.e. the junction of pylorus and duodenum, which, in *Setonix*, corresponds roughly with the point of closest adhesion by the mesial fold, of the colon to the pyloric regions, is regarded as the point marking the distal end of right, and the beginning of left colon (text figs. 20 and 23).

In *Setonix* there is a well-defined flexure of the colon in the caudal part of the right hypochondrium, at the right end of the transpyloric plane (text figs. 18a and b, 20, 21, 23, 25, 26); this might be taken as a flexure between the two sections of the colon. However, it is considered: *Firstly*, that the right transpyloric flexure of the colon is, relative to other viscera, more variable in position than the point of closest adhesion of the mesial fold to the pylorus at the pyloric constriction. *Secondly*, that the definition of this flexure is variable, being quite sharp in some specimens, but in one being more in the nature of a gentle curve. The point of closest adhesion of the mesial fold together with the associated pyloric constriction is in all cases well defined. Thus, this flexure is considered unsuitable as a boundary between the two sections of the colon. It is 25 to 55 mm. cephalad to the point of closest adhesion.

The well defined free cephalic margin of the mesial fold, seen only where the latter extends dorsad over the pylorus to become continuous with the lesser omentum of the stomach (text fig. 23), may provide a second suitable division of the colon into two parts. This margin does not vary in its relative position and, as will be discussed later, marks the point of continuity



Text fig. 21.—*S. brachyurus*. Ventral view of ileo-caecal region together with right colon and proximal part of left colon. $\frac{1}{2}$ natural size.

Abbreviations—see text figs 18a, 18b, 18c and 19.

of the greater omentum (associated with the left colon) with the mesial fold (associated with the right colon). Though this continuity of greater omentum and mesial fold is not seen in all marsupials, in some, including *Setonix*, it may provide a suitable morphological division of the colon. This free cephalic margin is 25 to 35 mm. cephalad to the point of closest adhesion, and up to 25 mm. caudad to the right hypochondrial flexure of the colon.

Mackenzie (1918b, p. 43) recognises a proximal portion of the left colon, which, owing to the fact that it and its mesocolon have been included in the greater omentum, lies close to the greater curvature of the stomach. In *Setonix* the left colon has a well defined left lumbar flexure just ventral to the caudal end of the left kidney (text figs. 18c, 20, 26, 29). It so happens that, owing to the simplicity of the gut pattern in *Setonix*, nearly the whole of the left colon from its right hand junction with the right colon to this left lumbar flexure, is associated with the greater omentum; on the right the greater omentum is

attached to the colon itself and to the left, losing this attachment, it adheres to the mesocolon (text figs. 26); thus, apart from Mackenzie's division of the left colon into proximal and distal parts, by reference to the adhesion of the greater omentum to the colon or its mesocolon, this left lumbar flexure forms a convenient well defined boundary between the proximal and distal parts of the left colon. It is realised that this condition is peculiar to *Setonix* and any other form which may have a simple hind-gut.

There are, then, two flexures of left distal colon, one on the right side of transpyloric plane (right hypochondrial), the other in mid-left lumbar region.

Distal part of left colon extends caudad to pelvic cavity, where it passes into rectum (text fig. 29). Loss of the mesocolic support of hind-gut in pelvic region, separates colon, which has this support, from rectum, which lacks it.

The position of the colon *in situ* will be considered under its various divisions.

The rectum is considered on pp. 128-140.

2. *Right (proximal) colon* (text figs. 18a and b, 20-25).

a. *Position in situ* (text figs. 18a and b).

Right colon is quite straight throughout its course, showing no signs of sacculation or of *ansa coli dextra*. (For terminology see Beddard, 1908, pp. 593-594 and fig. 123; Mitchell, 1916, p. 187 and pp. 193-199).

The aberrant condition of proximal part of colon of specimen 6 has already been referred to (see pp. 99 and 102 and text fig. 22).

Right colon lies ventral to duodenum, but in the right dorso-lateral part of abdomen, and extends through the right lumbar region from the trans-tubercular almost to the trans-pyloric plane.

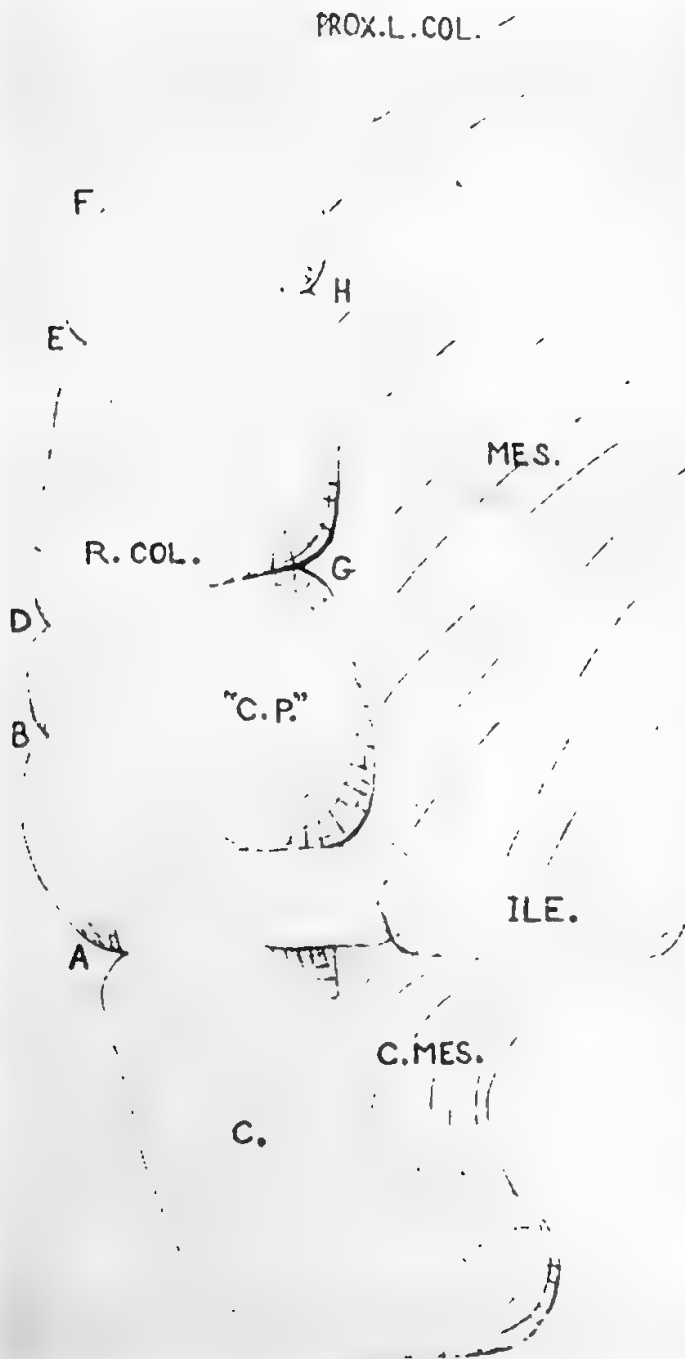
b. Dimensions.

Length of right colon, 35 to 50 mm. In adult right colon is not circular in section, but flattened laterally. It is greater in calibre than any other part of intestine, its circumference at proximal end (ileo-colic junction) being 80 to 100 mm. It narrows very slightly towards distal end, where the circumference is 70-90 m.m. In four specimens the maximum circumference was a few millimetres distad of ileo-colic junction; in two the maximum was nearer distal end. This variation may be partly due to variation in the distribution of the vegetable matter in this part of the hind-gut. Reference is again made to the immature male animal in which the right colon, empty of food, was narrow and contracted and more nearly uniform in bore throughout than in other specimens (see also p. 104).

c. Support.

Fixation of right colon within abdominal cavity is effected by:

- i. The mesentery (text figs. 21 and 22) along portions

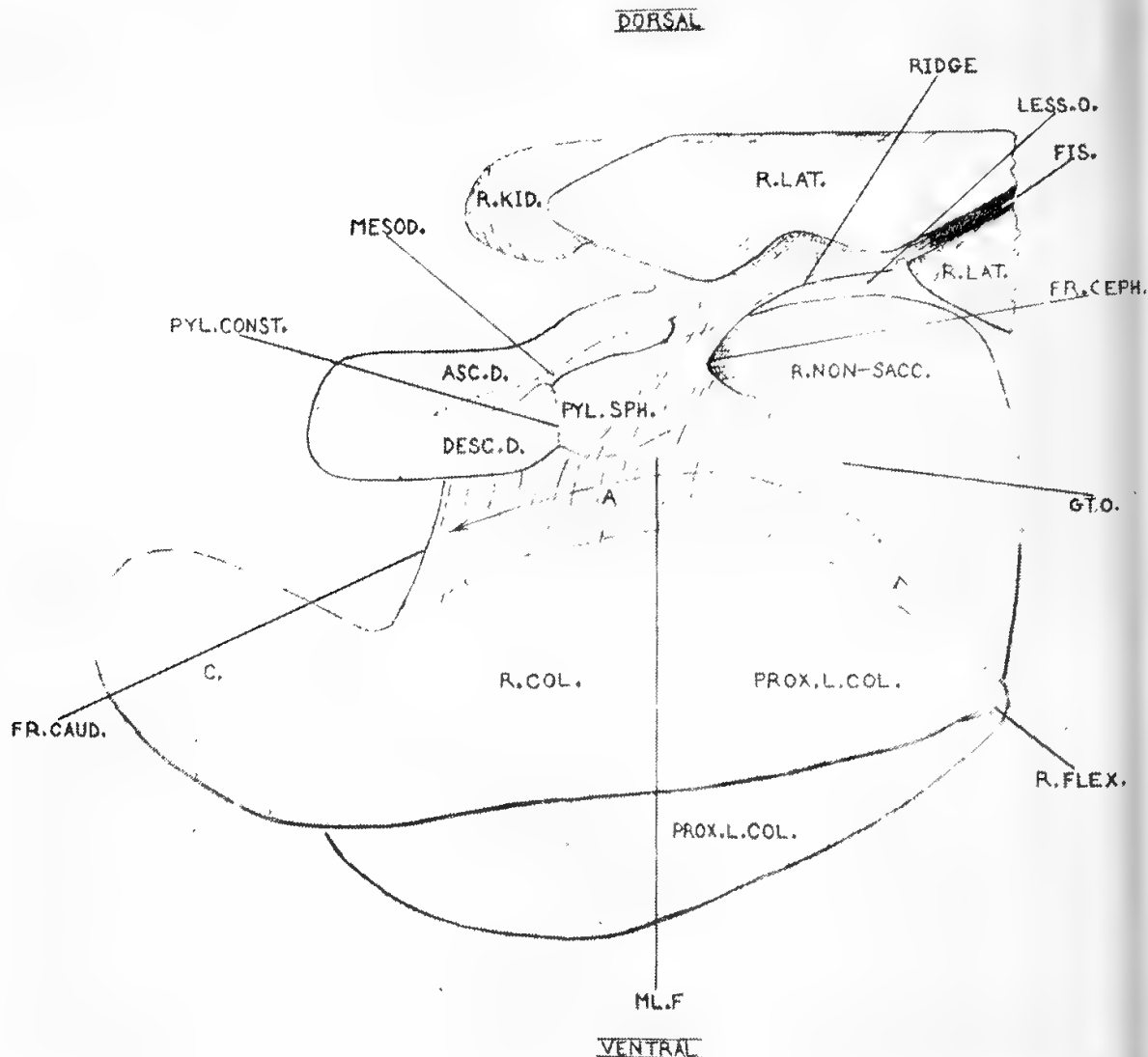


Text fig. 22.—*S. brachyurus*. Ventral view of ileo-caecal region, right, and proximal part of left colon of the aberrant specimen 6. Natural size.

A—constriction at proximal (basal) end of caecum; B, D-H, constriction of proximal part of colon; C.P.—sacculus on proximal part of right colon corresponding in position to Mitchell's "caecal pouch." Other abbreviations—see text figs. 18a, 18b, 18c, and 19.

of the edge of which the right colon, and in another sector the small intestine, is suspended.

- ii. The mesial fold (text figs. 23-25)—which is a sheet of peritoneum extending between distal two-thirds or more of right colon and proximal half to two-thirds of descending limb of duodenum, together with distal portion of pylorus (text fig. 23).



Text fig. 23.—*S. brachyurus*. Right lateral view of colico-duodenal and colico-pyloric regions with the associated peritoneal structures. The viscera have been displaced slightly ventrad. Arrow indicates right hand caudal prolongation of the lesser sac. 2/3 natural size. A—region of closest adhesion of colon to duodenum; ASC.D.—ascending limb of duodenum; DESC.D.—descending limb of duodenum; FIS—fissure dividing right lateral lobe of liver into two parts; FR.CAUD.—free caudal margin of mesial fold; FR.CEPH.—free cephalic margin of mesial fold; GT.O.—right hand end of greater omentum; LESS.O.—lesser omentum; MESOD—mesoduodenum; ML.F.—Meisal fold; PYL.CONST.—pyloric constriction (junction of pylorus and duodenum); PYL.SPH.—pyloric sphincter; RIDGE—continuation of free cephalic margin of mesial fold to fissure dividing right lateral lobe of liver in two. Other abbreviations—see text figs. 18a and b.

- (a) Margins—Mesial fold may be considered to have four margins:—

- (i) Colonic: attached to right colon. Length of attachment varies from individual to individual. It usually involves at least the distal two-thirds, even the whole of right colon.
- (ii) Duodenal-pyloric: attached to the descending limb of duodenum and to distal part of pylorus. Length of attachment varies from specimen to specimen, extending along proximal half to two-thirds of descending limb.

Its attachment to pylorus is to its outer right hand side.

Near the pyloric constriction (junction of pylorus and duodenum) the attachment (really a reflection of peritoneum from the gut) moves from outer side of this part of gut across ventral aspect of descending limb, and extends to inner angle of bend in duodenum (text fig. 24).

- (iii) Free caudal: which represents caudal limit of band and, when stretched, may be concave. Extends from inner angle of bend of duodenum to proximal part of right colon.

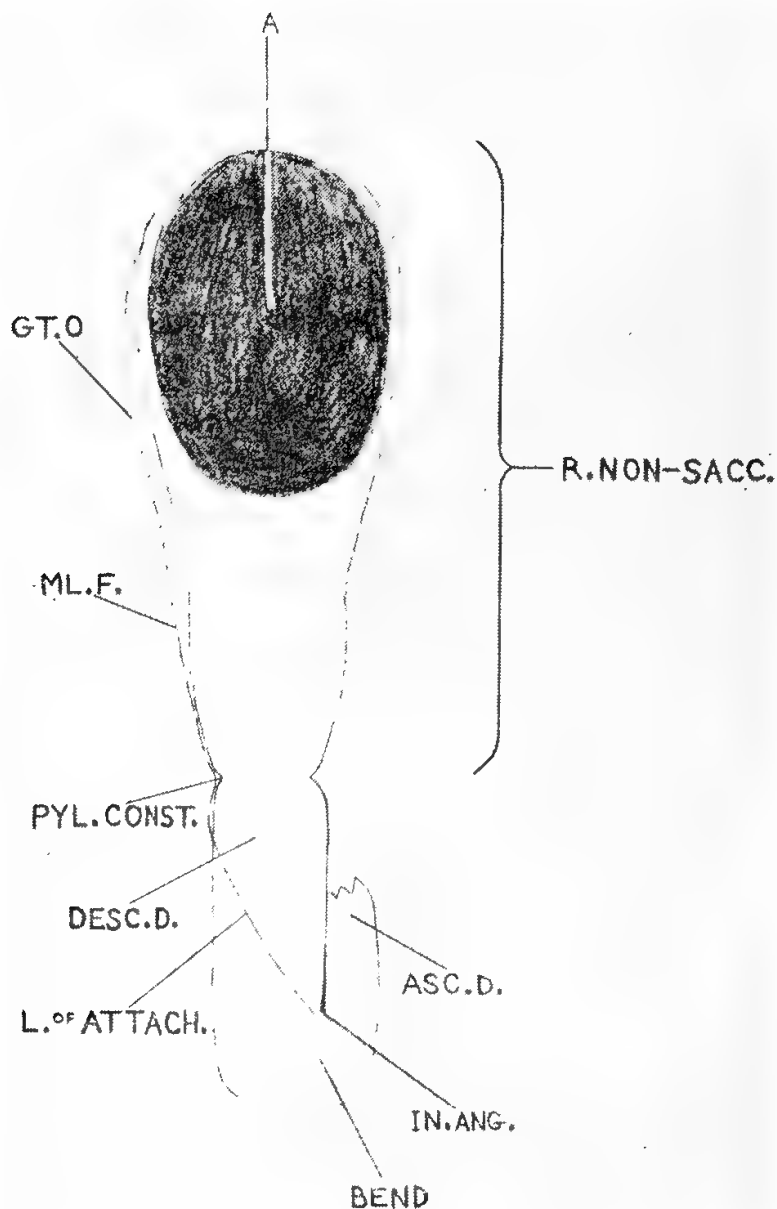
There is a cavity between mesial fold on the right, mesentery on the left, pylorus and descending limb of the duodenum dorsad and right colon ventrad.

Because of the continuity between mesial fold and greater omentum, this cavity is continuous with the lesser sac, of which it may be regarded as a right hand, caudal prolongation (arrow, text fig. 23). This prolongation of the lesser sac is closed caudad. The method of closure may be explained in one of two ways—which is correct I am not yet certain (text fig. 25).

The first explanation is that the mesoduodenum in the region of the bend of the duodenum, extends ventrad and to the left to become continuous with both the mesentery of the right colon and the caudal end of the mesial fold. The distinct free caudal margin of the mesial fold, which runs dorso-ventrad (vertically), is produced by this extension of the mesoduodenum to meet the mesial fold at an acute angle. The intersection of these two layers of peritoneum produces a posteriorly-directed "apex" of this right hand caudal prolongation of the lesser sac, closing it posteriorly.

The second explanation is that the mesial fold may be regarded as having two sheets, a long descending right hand one and a short ascending

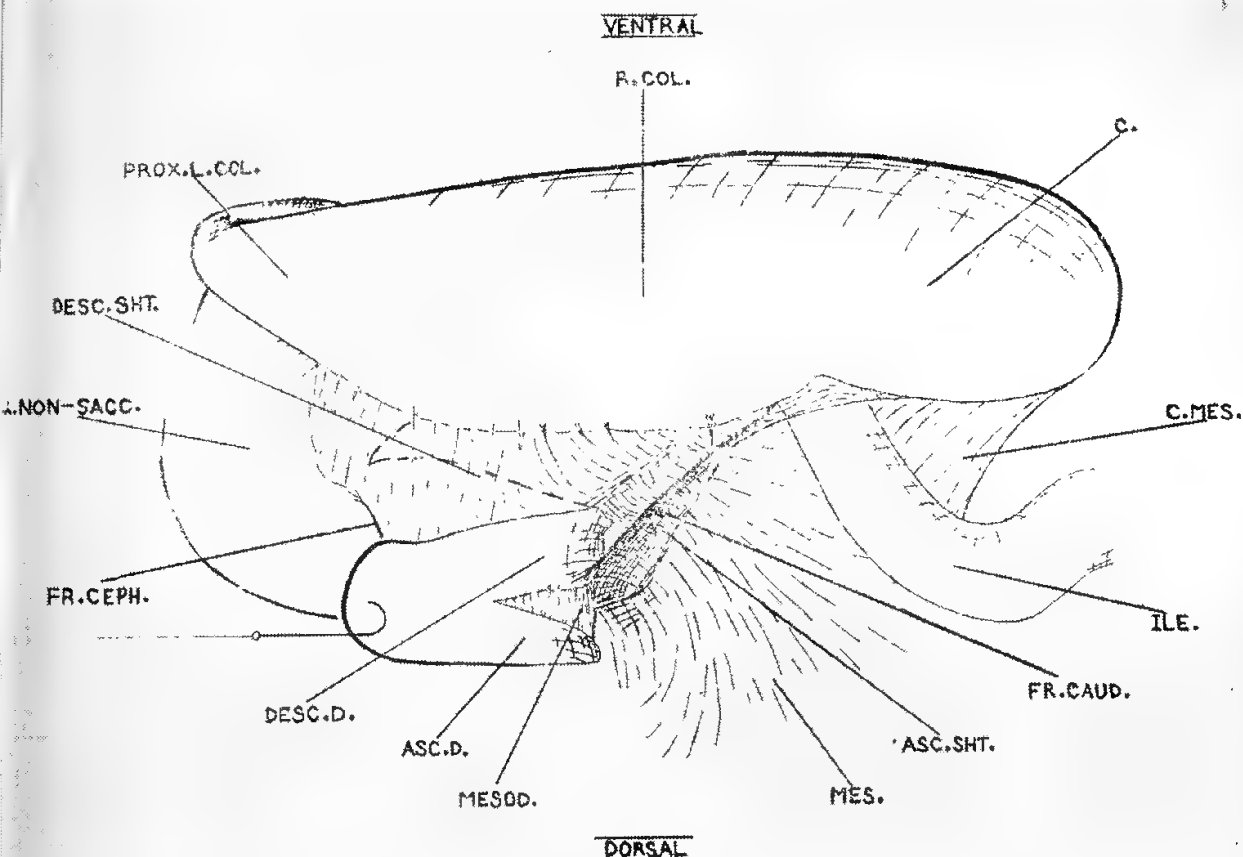
left hand one, closely related to each other and lying in a vertical (dorso-ventral) plane. That part of the mesial fold, already described as extending between colon ventrad and duodenum and pylorus dorsad, is regarded as the descending (right hand) sheet: this runs from the pyloric



Text fig. 24.—*S. brachyurus*. Semi diagrammatic ventral view of distal part of pyloric region of stomach and the duodenum, showing adhesion of mesial fold to duodenum and continuity between the cephalic end of this fold and right end of greater omentum. All other viscera omitted. Natural size. At A—rest of stomach removed by a horizontal section at its flexure in the right hypochondrium; BEND.—bend in duodenum; IN. ANG.—inner angle of bend in duodenum; L. OF ATTACH.—line of attachment of caudal part of mesial fold to descending duodenum. Other abbreviations—see text figs. 18a and 23.

region caudad as far as proximal end of right colon, where, co-incident with bending of duodenum to differentiate descending and ascending limbs, the mesial fold may be imagined to turn sharply to the left and run cephalad as the short ascending sheet. The ascending sheet becomes continuous at its cephalic end with the mesentery and the mesoduodenum. The caudal free margin of the mesial fold is formed where the descending sheet changes to the ascending one, thus closing the right hand prolongation of the lesser sac caudad (see also under *M. eugenii*).

- (iv) Free cephalic—is seen where mesial fold extends dorsad over pylorus to become continuous with the lesser omentum. It has a definable length of 20 to 30 mm. and, along this length, is free from adhesions to other structures. A ridge, representing a continuation of this free margin, can



Text fig. 25.—*S. brachyurus*. Right lateral view of colico-duodenal and colico-pyloric region to show method of closure of right hand caudal prolongation of lesser sac (see p. 111). The duodenum has been folded forward over distal part of pyloric part of stomach, the "bend" having been pulled cephalad. 2/3 natural size.

ASC.SHT.—extension of mesoduodenum near bend of duodenum to mesentery and caudal end of mesial fold, or, alternatively, the short ascending left hand sheet of mesial fold, closing right hand caudal prolongation of lesser sac; DESC.SHT.mesial fold or "long descending right hand sheet." Other abbreviation—see text figs. 18a, 19 and 23.

be traced to fissure dividing right lateral lobe of liver in two (text fig. 23). The definition of the free cephalic margin of the band is lost after crossing pylorus to join lesser omentum dorsad, and as it approaches the colon ventrad.

Owing to the considerable transverse (right to left) extent of greater omentum, and to cephalo-caudal length of mesial fold, the latter, in the region of its free cephalic margin, becomes continuous with the greater omentum. This continuity explains, firstly, the loss of definition of the free cephalic margin of mesial fold as it approaches the right colon, having crossed the pylorus, and, secondly, the formation of a right caudal prolongation of the lesser sac. In an adult male *Trichosurus vulpecula*, the mesial fold and greater omentum were not so well developed and were not continuous. Thus the lesser sac was sealed off and had no right caudal prolongation. The continuity between the mesial fold and the right end of the greater omentum, and the mesial fold and the lesser omentum in *Setonix*, means that, in effect, the greater omentum is continuous with the lesser (see also Mackenzie, 1918b, 41).

- (b) Width of mesial fold—free width of mesial fold at its caudal extremity, 30 to 40 mm. This is the maximum distance between right colon and duodenum in this region. Cephalad the band gradually narrows so that in region of pyloric constriction its free width is 20 to 25 mm. The "free" width has been emphasised; the band, is of course, continued over the duodenum and pyloric sphincter as part of visceral layer of peritoneum. It can only be freed from duodenum and sphincter by careful dissection.

Where the mesial fold extends dorsad from greater omentum over pylorus to lesser omentum (cephalad to the pyloric sphincter), it loses adhesion to right (outer, lateral) wall of pylorus. Extent of this freeing of mesial fold varies a little from specimen to specimen. Associated with this dorsal prolongation of mesial fold to lesser omentum, is the well defined free cephalic margin of mesial fold seen where the latter crosses the pylorus. This has been described above. Thus there is a band which is 10 to 15 mm. wide and part of the mesial fold, extending from the greater to the lesser omentum.

d. Conclusion on right colon.

Thus in *Setonix* the right colon (particularly its distal portion) is close to the pylorus and duodenum. This is in accord with previous general and particular descriptions. Flower (1872, pp. 291-294) and Mitchell (1916, p. 186 and Figs. 1A and B) have recognised that the beginning of the hind-gut and the

duodenal region of mammals, tend to be close to each other. Klaatsch (1892, pp. 662-664) describes how the hind-gut with its "Flexura coli dextra." overlies the duodenum in *Halmaturus*. He says that in the region of the ligamentum cavoduodenale, connections are hinted between the duodenum and hindgut. He also claims that the colon approaches the duodenum in *Phalangista vulpina* (*Trichosurus vulpecula*). The views of Beddard (1908) and Mackenzie (1918b) on the subject of adhesions between the colon and duodenum, have been discussed on page 94 of this paper.

Mackenzie seems to recognise two separate adhesions in the colico-duodenal region—one which "passes across the thickened pyloric sphincter of the stomach from the right of the lesser to the right of the greater omentum" another which he describes thus, "We frequently see a peritoneal adhesion or band from the dextral margin of the right free colon to the descending duodenum, even as far as its lower third" (1918b, pp. 41 and 45). The inference is that there are two distinct bands of peritoneum, one extending between colon and pylorus, the other between colon and duodenum. The total extent of these two bands is the same as the single one described above for *Setonix*.

Any differentiation of the single band in *Setonix* which might lead one to conclude that it arose as two separate structures, appears to be lacking in the specimens which I have examined. *Setonix* may therefore differ from the macropods examined by Mackenzie; his two (inferred) fold in the colico-duodenal region may be distinct in intrauterine and pouch embryos of *Setonix*, but if so, they lose their separate identities in the adult.

The structure of the right colon in *Setonix* is, in a broad way, as Mackenzie (1918b, pp. 41-5) describes it for macropods generally, the only marked difference being that noted above.

3. Left (distal) colon (text figs. 18a and c; 20, 21; 26-29).

a. As a whole.

- i. Position *in situ* (text figs. 18a and c; 20)—Generalised plan of left colon of *Setonix* is 7-shaped (text fig. 20). Beginning on right side of abdomen, where it is continuous with right colon, the left colon runs through the cephalic part of right lumbar region. At right side of transpyloric plane, near the bend within the right hypochondrium of lesser curvature of stomach, the left colon flexes sharply, running to the left across abdomen into the mid-left lumbar region (text figs. 18a and b). In left lumbar region, usually just ventrad to caudal end of left kidney, left colon flexes through about 90°, to run caudad into pelvic cavity, where it becomes continuous with rectum (text figs. 18c, 20, 26 and 29).
- ii. Dimensions. Total length of left colon, excluding rectum, 350 to 410 mm. As has been mentioned, its calibre varies, depending on the amount of faecal matter it contains. At

its proximal end, where it is continuous with right colon, the circumference is 70 to 90 mm. There is considerable reduction in calibre at flexure at right end of transpyloric plane, where the circumference may be only 10 to 20 mm. Distad of this flexure the maximum circumference may be 60 mm. and the minimum, measured on left colon as it approaches pelvis, and in a contracted condition, 20 mm.

- iii. Support (text figs. 26-29). Whole of left colon is suspended on edge of mesocolon. In addition, proximal part of left colon, or its mesocolon, has additional support from the greater omentum, considerably reducing its mobility (text figs. 26-28). If left colon is considered to begin at the point of its closest adhesion to duodenum by means of mesial fold, then, since the mesial fold is continued cephalad beyond this point, the fold must be considered as attached to the first 25 to 35 mm. of the left colon

- b. Proximal part of left colon (text figs. 18a, b and c; 20; 26-29).

- i. *In situ* (text figs. 18a, b and c)—From its junction with right colon, ventral to pyloric sphincter, the proximal part of left colon extends through cephalic part of right lumbar region. At right end of transpyloric plane it flexes sharply to run more or less transversely across abdomen, following the greater curvature of the stomach, into the left lumbar region. Here there is the sharp caudal flexure differentiating the distal part of the left colon.

From its course in the abdominal cavity this part of the colon in *Setonix* may be called a "transverse colon." Proximal two-thirds of "transverse colon," lying close to right oblique limb of stomach, runs with a slight ventral component caudad and to the left (text fig. 18b). Close to apex of stomach, in caudal part of "umbilical" region (see Mackenzie 1918b, pp. 29-30), the "transverse colon" curves dorsad, running to the left lumbar flexure of the colon (text figs. 18a and c).

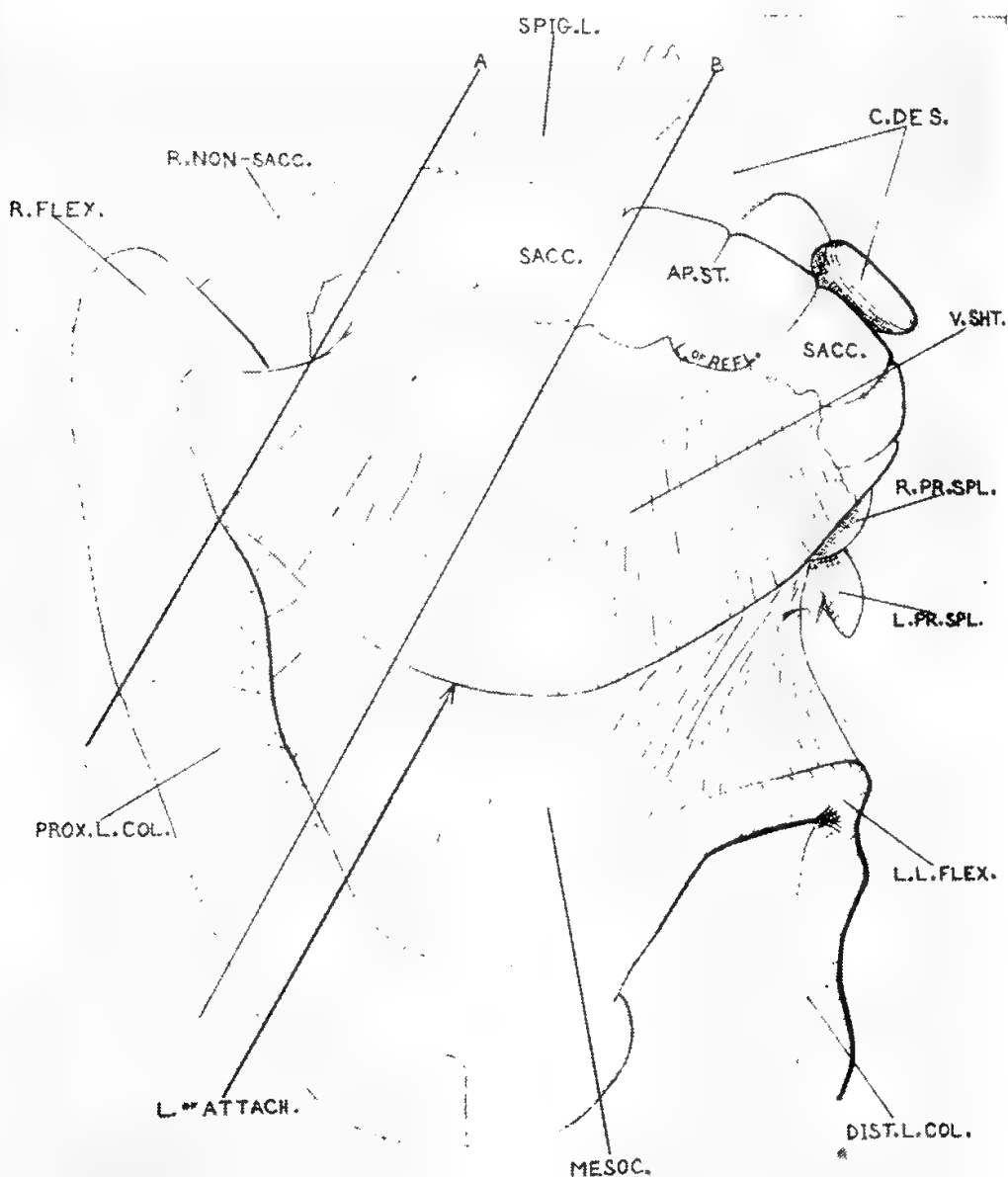
- ii. Dimension—Proximal part of left colon is between 250 and 320 mm. long, 23 to 50 mm. of this being in cephalic part of the right lumbar region. At right hypochondrial flexure the calibre is greatly reduced so that the circumference of colon is between 10 and 20 mm. (cp. max. calibre, p. 115). At a point just proximal to left lumbar flexure of left colon, the circumference of the contracted and empty colon is about 25 mm.

In some animals faecal pellets were constricted off halfway along the "transverse colon" (text fig. 29).

- iii. Support (text figs. 26-29). Fixation of proximal part of left colon is effected—
 - (a) By greater omentum (text fig. 26-28), the ventral sheet (descending or anterior sheet of human anatomy) of which is attached to right hand 60 to 80 mm. of

"transverse" colon. Farther to the left, the greater omentum, no longer attached to colon itself, adheres to mesocolon of proximal part of left colon as far to the left as its left lumbar flexure (text figs 26).

The portion of proximal part of "transverse colon" to which greater omentum is attached, is closely bound to



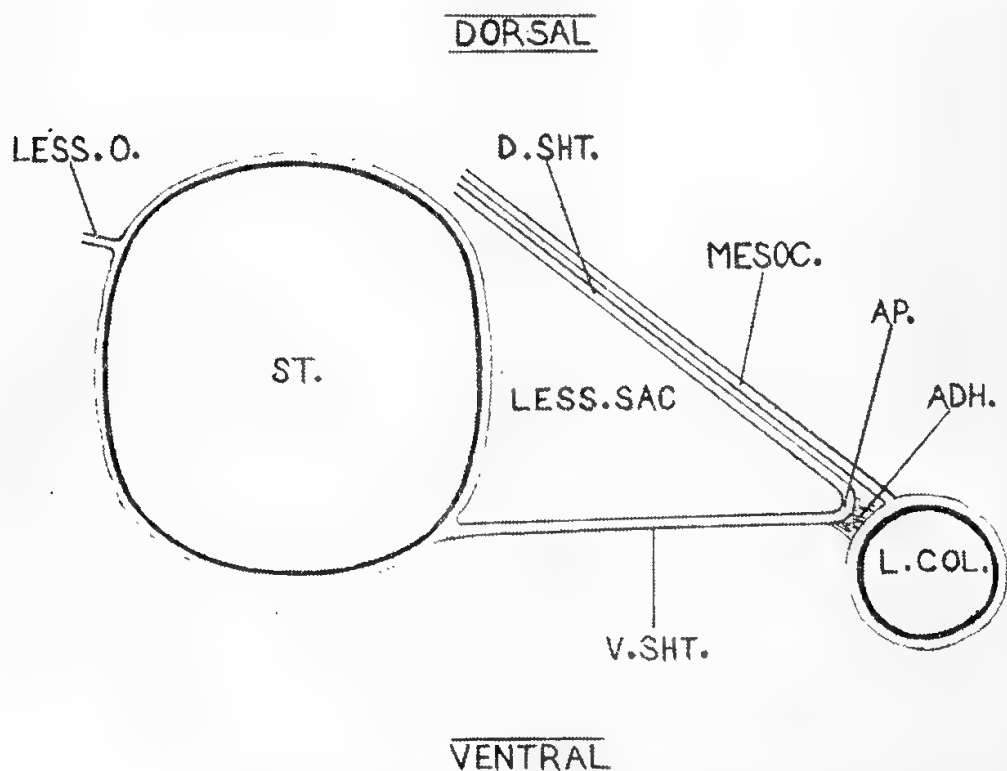
Text Fig. 26.—*S. brachyurus*. Ventral view of proximal part of left colon ("transverse colon") with associated greater omentum and mesocolon. Note considerable accumulation of faecal matter in proximal two-thirds of "transverse colon." In order to stretch and show clearly the mesocolon and greater omentum, the stomach has been pulled forward and the "transverse colon" back. 2/3 natural size.

A—approximate line of section for text fig. 27; B—approximate line of section for text fig. 28; L. OF ATTACH.—line of attachment (adhesion) of ventral sheet of greater omentum to mesocolon; L. OF REFL.—line of reflection of greater omentum (ventral sheet from greater curvature of stomach; V.SHT.—ventral (descending) sheet of greater omentum. Other abbreviations—see principally text fig. 18a; also text fig. 18b, 18c and 20.

distal half of right oblique limb of stomach. (This limb extends obliquely across abdomen from left lumbar region to right hypochondrium, and includes all the non-sacculated part of the stomach before its bend in the right hypochondrium, and a small portion—maximum of 35 mm.—of the distal part of the sacculated portion of the stomach).

In *Setonix* the inclusion of the proximal part of the transverse colon" in the lesser sac appears to be as follows—the caudad directed apex of the bag-like growth which forms the greater omentum, does not quite reach the left colon, but, falling a few millimetres short, sends out secondary connective tissue attachments to colon. Dorsal sheet of greater omentum (posterior or ascending sheet of human anatomy) is in close contact with mesocolon of "transverse colon," both where greater omentum is attached to colon itself and where it adheres to the mesocolon (text fig. 27).

The approximation of right hand portion of "trans-



Text fig. 27.—*S. brachyurus*. Diagrammatic transverse section through stomach and adjacent proximal part of left colon ("transverse colon"), showing relationship between greater omentum, mesocolon and "transverse colon." Line of section at A in text fig. 26. Figure also applies to first limb of left colon of *M. eugenii*. About natural size.

AP.—caudad directed apex of bag-like outgrowth formed by greater omentum; ADH.—connective tissue adhesion between apex of this bag and "transverse colon"; D.SHT.—dorsal (ascending) sheet of greater omentum; LESS.SAC.—lesser sac; ST.—stomach. Other abbreviations— see text figs. 18a and c, 23 and 26.

verse colon" to greater curvature of stomach, through the adhesion of the greater omentum, is closest on the right, where the greater omentum and the mesial fold are continuous (text fig. 26). At this point the distance between stomach and colon is 35 to 50 mm. (i.e. here the ventral sheet of the greater omentum is 35 to 50 mm. wide). The maximum displacement of "transverse colon" from greater curvature, without damage to the greater omentum or mesocolon, increases to the left, so that where the attachment of greater omentum to "transverse colon" is finally lost, at a point between 60 and 80 mm. along the latter, the displacement is between 55 and 65 mm. (i.e. at this point the width of the ventral sheet of the great omentum is between 55 and 65 mm.).

The separation, then, of the left colon from the greater curvature of the stomach is fairly gradual (see text fig. 26 and cf. *M. eugenii* in later note).

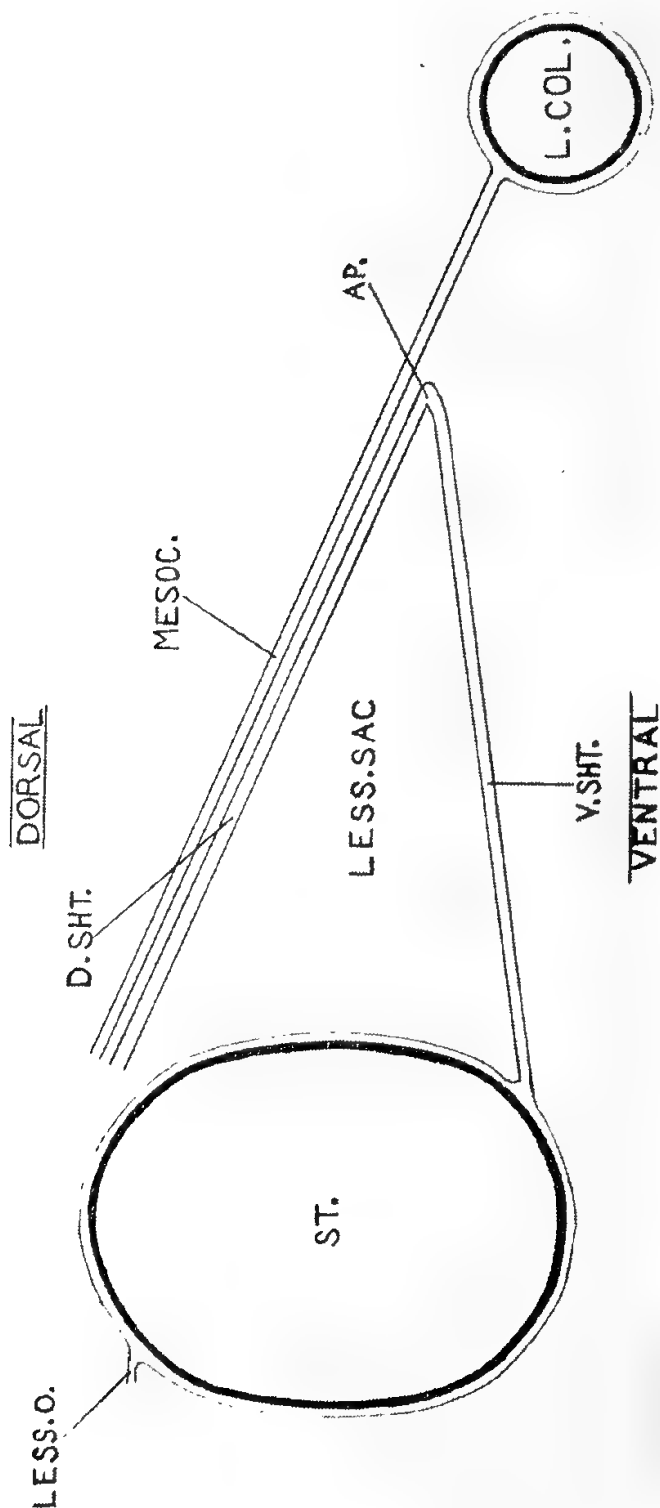
Maximum width of greater omentum (65 to 90 mm.). is at a point 10 to 30 mm. distad of apex of stomach along the latter's right oblique limb. Farther to the left, width of ventral sheet of greater omentum decreases, so that, at caudal end of body of spleen, which is supported from greater curvature of stomach by greater omentum, the width is between 15 and 25 mm.

Thus, on either side of the point of maximum width of the ventral sheet its width decreases to between 36 and 50 mm. on its extreme right, and 15 and 25 mm. on its extreme left (text fig. 26).

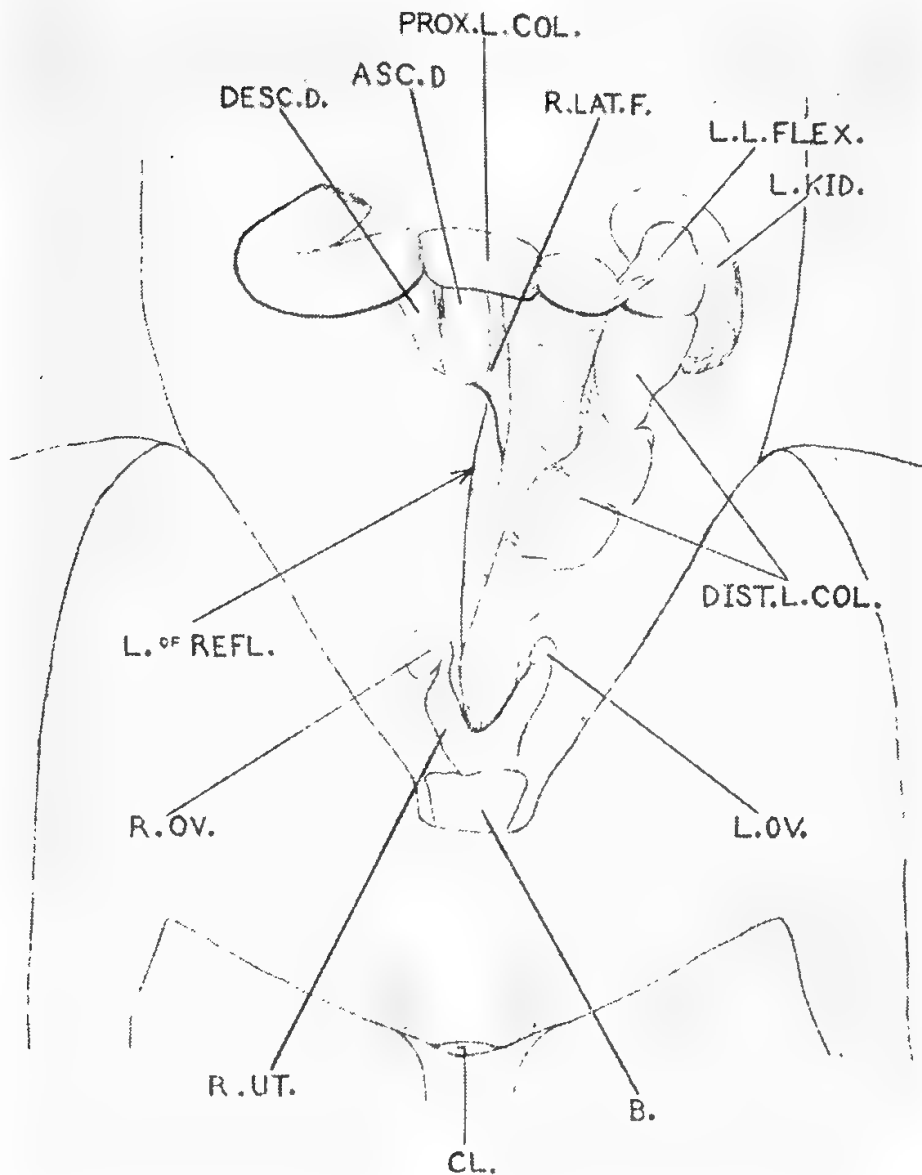
- (b) By mesocolon (text figs. 26-28)—Mesocolon, supporting the whole of proximal part of left colon, is, broadly speaking, fan-shaped, the focus of the fan being in middle line of dorsal abdominal wall, level with cephalic end of left kidney.

Mesocolon of "transverse colon" reaches a maximum width of between 100 and 130 mm. at that part of the proximal portion of left colon near apex of stomach. At right and left ends of "transverse colon" the mesocolon is narrower (75 to 90 mm. wide).

- iv. Conclusion on proximal part of left colon. The close relationship through the growth of the mesial fold, between right hand end of left colon and distal part of greater curvature of stomach (pylorus and duodenum), facilitates the extension and final adhesion of the greater omentum, arising from the greater curvature, to the proximal part of the left colon. However, the "influence" of the mesial fold's adhesion is gradually lost to the left. The greater omentum loses its adhesion to the left colon and is attached to the mesocolon



Text fig. 28.—*S. brachyurus*. Diagrammatic section through stomach and adjacent left colon ("transverse colon") showing relationship between greater omentum, mesocolon and "transverse colon." Apex of bag formed by outgrowth of greater omentum falls short of left colon, but adheres to mesocolon. Line of section at B in text fig. 26. Figure can apply to a very limited section in *M. eugenii*—after loss of direct adhesion of greater omentum to first limb of left colon (between X and Y, text fig. 30) (see p. 124). About natural size. Abbreviations—see text figs. 18a, 18c, 23, 26 and 27.



Text fig. 29.—*S. brachyurus*. Ventral view of proximal (transverse) and distal parts of left colon. Notice the formation of distinct faecal pellets in the "transverse" colon, as well as in the distal part of the left colon. $\frac{1}{2}$ natural size.

L.O.V.—left ovary; L. OF REFL.—line of reflection of mesocolon of distal part of left colon from dorsal body wall; R.LAT.F.—right lateral (duodeno-mesocolic) fold; R.OV.—right ovary; R.UT.—right uterus. Other abbreviations—see text figs. 10, 18b and c, 20 and 23.

of the "transverse colon" as far to the left as the left lumbar flexure. The line of this attachment can be traced to the left for 80 to 140 mm., finally losing definition as it approaches the spleen. It diverges on the left from the line of attachment of the mesocolon to the "transverse colon" (text fig. 26). In the region of the apex of the stomach, where the ventral sheet of the greater omentum is wide, the divergence reaches a maximum of between 40 and 50 mm. This maximum divergence seems to be related in part to the great width of the mesocolon at this point, where the "transverse colon" will have a maximum mobility and maximum possible displacement from the greater curvature of the stomach. In spite of the width of the greater omentum at this point, it falls far short of the left colon. Farther to the left, in region of left lumbar flexure of colon, where the mesocolon is narrower, the divergence is less—30 to 45 mm. It is because of the loss of "influence" of the mesial fold to the left and the increased width of the mesocolon at the point of greatest width of the greater omentum, that the latter loses its adhesion to the colon and is attached to the mesocolon instead.

Flower recognises that the adhesion, in some mammals, between the transverse mesocolon and the greater omentum, is due to close connection between the right end of the transverse colon and the pyloric end of the stomach (1872, pp. 293-294).

Beddard (1908, p. 593 and fig. 122) indicates an attachment of the greater omentum to the colon in his Stage 11B, but does not refer in that case to a colico-duodenal ligament. However, in his Stage 111, as well as an attachment of the greater omentum to the left colon, he shows a colico-duodenal ligament. In this respect Stage 111 resembles the condition in *Setonix*.

c. Distal part of left colon (text figs. 20 and 29).

- i. *In situ* (text fig. 29)—When seen *in situ*, the distal part of left colon gradually approaches the middle line as it passes caudad from left lumbar flexure to pelvis and rectum. It shows no signs of loops (*ansae coli*).
- ii. Dimensions—Distal part of left colon is between 70 and 90 mm. in length, its circumference being between 20 and 50 mm., the variation being due to the amount of distension by faecal matter.
- iii. Support (text fig. 29)—It is suspended on edge of mesocolon, which is reflected from middle line of dorsal abdominal wall. Length of reflection (attachment) is between 110 and 135 mm. Width of mesocolon at the left lumbar flexure between 25 and 35 mm., while halfway between left lumbar flexure and rectum it is between 5 and 16 mm. Rectum is without mesocolic support. Thus the mesocolon narrows

caudad, the distal part of left colon having maximum mobility at its cephalic end near left lumbar flexure, the mobility decreasing as it travels through caudal part of abdominal cavity to rectum. Owing to bulk of surrounding coils of small intestine, the mesocolon of distal part of left colon does not hang in a vertical sheet from the mid-dorsal line, but is folded over to the left (text fig. 29): correspondingly colon is displaced to the left, the displacement being a maximum at its cephalic end, associated with its greater mobility in this region. As the mobility decreases caudad, so does the lateral displacement, until, within the greater (false) pelvis, the distal part of left colon hangs vertically from mid-dorsal line at the edge of the narrowed mesocolon. This change in attitude is due to decrease in the bulk of the surrounding viscera and to the narrowing of the mesocolon.

4. *Preliminary note on colon of **Macropus eugenii** (text figs. 30 and 31).*

a. Mesial fold.

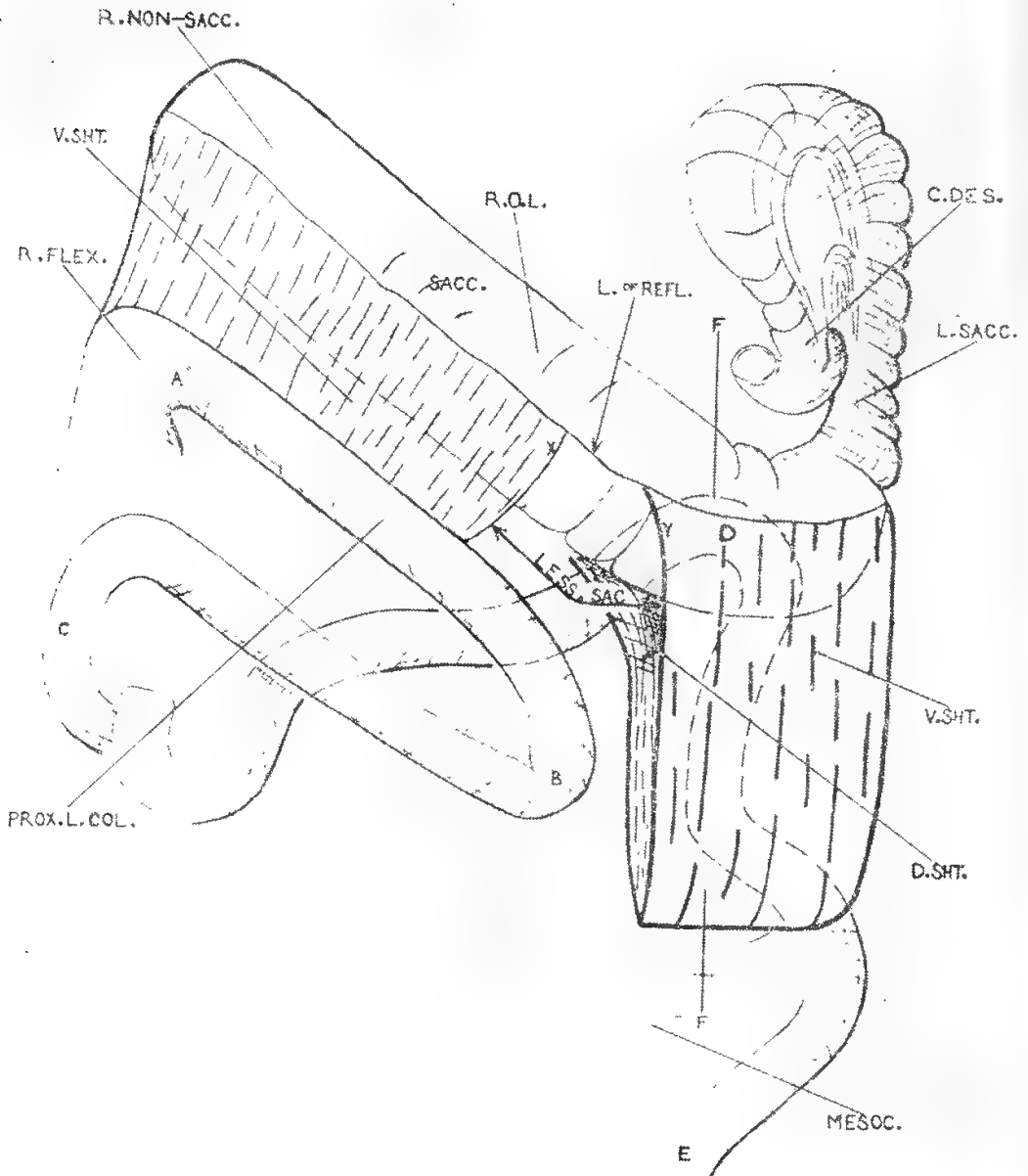
Mesial fold well developed and binds right colon closely to pylorus and duodenum. This binding appears to be closer than in *Setonix*. The fold is continuous with right hand extreme of ventral sheet of greater omentum. Thus, as in *Setonix*, there is a blind, right hand, caudal prolongation of the lesser sac.

b. Colon.

Right colon simple and without signs of ansa coli dextra. My brief examination does not show that, apart from size, it differs from that of *Setonix*. There is a flexure at right end of transpyloric plane. Total length of left colon is about 800 mm., greater than in *Setonix*, but this is not unexpected, since the animal is noticeably larger. However, the pattern of the gut is very different. It shows a well developed ansa coli sinistra and may be considered to have at least four limbs (text fig. 30).

First limb extends from the junction with the right colon to the left for about 130 mm. and is close to the greater curvature of stomach. Left colon then flexes on itself and extends back to right end of transpyloric plane as the *second* limb, which is also about 130 mm. long. This limb has minor undulations. At right end of transpyloric plane left colon flexes back to the left rather gently, and thus is formed the *third* limb which is about 400 mm. long and, indirectly, extends across cephalic part of abdominal cavity to the left lumbar region, dorsal to the first 260 mm. of the left colon. It has several fairly well defined undulations along its length. In left lumbar region, left colon turns to run caudad for about 150 mm. as the *fourth* limb of left colon, becoming continuous with rectum on reaching the pelvic cavity. Its course is fairly straight, there being one incomplete loop along its length. Whole of left colon in *M. eugenii*, as in *Setonix*, is suspended from the edge of mesocolon. First limb of left colon is the only section to which the greater omentum is attached (text fig. 30). It is this attachment, and consequent immobility of this part of colon, which differentiates

it so clearly from the rest of left colon. It lies closer to greater curvature of stomach than does the corresponding part of the intestine in *Setonix*—the distance between the two parts in *M. eugenii* is not more than 25 mm. Loss of attachment of greater omentum to first limb corresponds approximately to the flexure between the first and second limbs. The greater omentum had been damaged just to the left of the point where it loses attach-



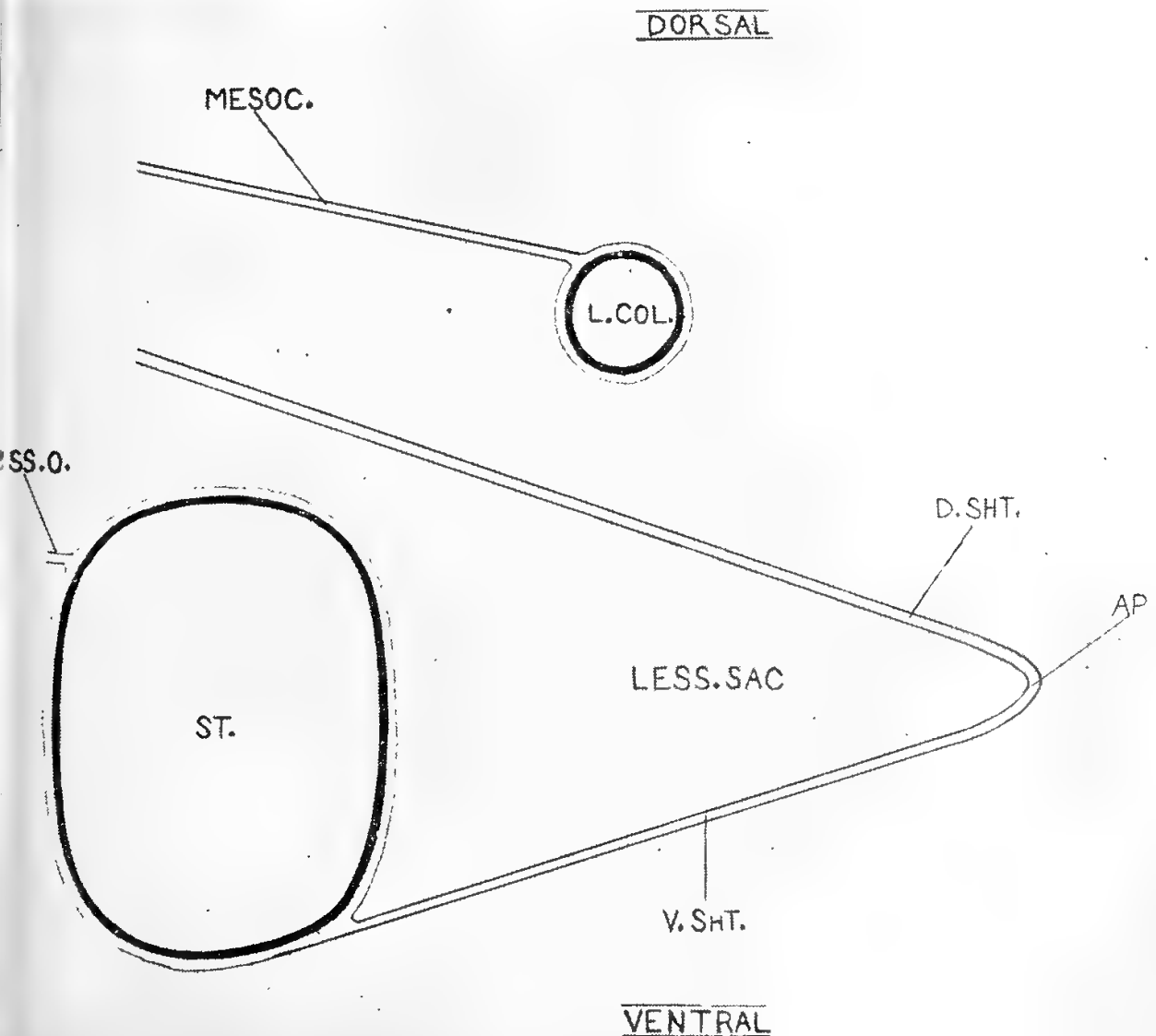
Text fig. 30.—*M. eugenii*. Ventral view of stomach and left colon with associated greater omentum. The left hand free portion of greater omentum has been emphasised. The mesocolon of fourth limb of left colon is shown. About $\frac{1}{2}$ natural size.

A-B—first limb of left colon (=Mackenzie's proximal part of left colon); B-C—second limb of left colon; C-D—third limb of left colon; C.D.E.S.—bifid cul-de-sac of cardiac extremity of stomach; D-E—fourth limb of left colon. At D—? homologue of left lumbar flexure of left colon of *Setonix*; F—approximate line of section for text fig. 31. Between X and Y—greater omentum damaged. Other abbreviations—see text figs. 18a, b and c, 26 and 27.

ment to colon, but it seems that separation of greater omentum and colon is quite abrupt. Greater omentum appeared to be attached to mesocolon for a short distance on the left of its loss of attachment to colon. It then loses all connection with colon and mesocolon (text figs. 30 and 31). First limb of left colon, being included in the greater omentum and lying close to greater curvature of stomach, is the proximal part of the left colon (Mackenzie 1918b, p. 43); the rest of the left colon, supported in the abdomen simply by mesocolon, is more mobile than first limb and is not close to greater curvature of stomach.

c. Greater omentum (text figs. 30 and 31).

On the right, the greater omentum is continuous with the mesial



Text fig. 31.—*M. eugenii*. Diagrammatic transverse section of stomach and left colon (third limb) showing relationship between greater omentum, mesocolon and left colon. Line of section at F in text fig. 30. Greater omentum in this region does not adhere to left colon or any part of mesocolon, which is relatively narrower than that of the corresponding region in *Setonix*. Natural size. Abbreviations—see text figs. 18a and c, 23, 26 and 27.

fold. It is also attached to a portion of left colon (first limb) and to a small section of mesocolon. Dorsal (ascending) sheet of this part of greater omentum is closely applied to mesocolon supporting the first limb of left colon. However its left hand half, at least, is completely free of attachments to left colon or to mesocolon, as it descends from stomach or ascends to dorsal abdominal wall. It hangs from the stomach in the form of a bag, the blind end of which points caudad.

5. *Conclusion on pattern of Colon of Setonix.*

There is some difference of opinion as to the existence of ansae coli and the colico-duodenal ligament in marsupials.

a. *Ansa coli.*

Beddard (1908 p. 575) says:—

"As a rule, with but few exceptions, the Marsupials possess none of those permanent loops of the colon which have been termed by Tullberg 'ansae coli,' and by Klaatsch 'flexurae coli.'"

However, he says he has seen signs of these colic loops in *Didelphys virginiana*, *Trichosurus vulpecula*, and in various species of *Macropus*, these genera presumably being the exceptions. His doubt about the existence of ansae coli in marsupials is indicated also in his description of the various basic patterns of the mammalian colon (1908, pp. 591-6; figs. 120-123). He includes *Macropus* in stages IIA and B, but excludes it from III, which has ansae coli. Mitchell, though he shows no ansae coli in the polyprotodonts, does figure them in the diprotodonts. He says, when speaking of wavy expansions or minor loops distal to the pendant loop in diprotodonts: "These are all supported by a simple expansion of the mesorectum and represent gradations from a merely expanded rectum to what would be regarded as a definite *ansa coli sinistra*." (1916, p. 119). Thus Mitchell in his figures and text, is far more definite as to the existence of ansae coli in marsupials, than is Beddard. Mitchell's observations on the existence of a pronounced *ansa coli sinistra* in macropods, are corroborated by mine on *M. eugenii*.

b. *Colico-duodenal ligament.*

Beddard mentions secondary connections between duodenum and colon in *Trichosurus*, which I have seen in an adult male *T. vulpecula*, and says that marsupials show indications of this third stage of evolution of intestinal pattern (1908, pp. 593-6; fig. 123). Stages IIA and B (pp. 592-3) including *Macropus* and other marsupials, lack the colico-duodenal adhesion shown in Stage III. If the mesial fold is the same structure as the colico-duodenal ligament, it seems strange that Beddard should not be more emphatic about its occurrence in marsupials. Mackenzie (1918b) has seen the structure in Macropods, the Koala and Wombat, and I believe I have found it strongly developed in *M. eugenii* and *Setonix*.

It is apparent from comparison of my illustrations with those of the colon of macropods given by Mitchell (1905, pp. 451-452, figs. 7 and 8; 1916, p. 198), and from my observations on the

colon of *M. eugenii*, that its pattern in *Setonix* is simple.

In the macropods, whose intestines are figured by Mitchell, and in *S. brachyurus* and *M. eugenii*, the right colon is quite straight and without any signs of *ansa coli dextra*.

It is the left distal colon of macropods that becomes complicated by minor loops, and so the simplicity of *Setonix* lies in its left colon. Comparison with the left colon of *M. eugenii*, which has a well developed *ansa coli sinistra*, accentuates the simplicity of the pattern in *Setonix*. The left colon of *Setonix*, with its two flexures (right and left) and two major limbs (a transverse proximal and a caudad directed distal one) (text fig. 20), may represent a simple *ansa coli sinistra*.

In *Setonix* the proximal part of the left colon extends transversely across the abdomen from right to left. In *M. eugenii* the proximal part of the left colon (in Mackenzie's sense) is relatively shorter and extends only part of the way across the abdomen; there is a flexure in the left lumbar region differentiating the third from the fourth limb of the left colon (see text fig. 30 and p. 123).

However the left lumbar flexure of *Setonix* is more striking than that of *M. eugenii*, which has other undulations and loops on the left colon obscuring it (cf. *Setonix*).

It is not clear to me whether the left lumbar flexure of the colon in *M. eugenii* is the same as that in *Setonix*; i.e. whether the part of the left colon in *M. eugenii* which has minor loops and extends indirectly from the right end of the transpyloric plane transversely across the abdomen to the left lumbar region, is homologous with the "transverse colon" of *Setonix*.

Associated with simplicity of gut pattern of *Setonix* is the extensive attachment of the greater omentum to either left colon or its mesocolon. This relationship may extend for almost the full width of the cephalic part of the abdomen, from the right proximal end of the left lumbar flexure.

In *M. eugenii* there is a relationship between the lengthening of the colon (the development of an *ansa coli sinistra*) and the relatively less extensive attachment of the greater omentum to the left colon or its mesocolon. In this animal the association does not extend the full width of the abdomen, but is confined to the right hand half (see pp. 123 and 124).

Investigation has shown that in *Setonix* and *M. eugenii* the greater omentum is attached to portions of the left colon and the mesocolon, and that each has a well developed mesial fold (colico-duodenal ligament). A ligamentum cavoduodenale (right lateral fold) is also developed in *Setonix* (text fig. 29) and *M. eugenii*. *M. eugenii* has an *ansa coli sinistra*, which *Setonix* may possess in a simplified form. Neither have an *ansa coli dextra*.

Beddard (1908, p. 594) says that there are "... simpler forms and more complexly convoluted colons" in Stage III. As both the above forms have points in common with Stage III, they

might be classified in that group as the "simpler forms" noted by Beddard. The colon of each certainly seems more complex than Stage IIB and if not strictly Stage III, is half way between it and IIB.

6. *The rectum and its peritoneal relations.*

I could find no account of the peritoneal relations of the pelvic viscera of marsupials in available literature. The identification of structures mentioned in my descriptions has been made by reference to Cunningham (1937) and Gray (1916). For details of the male urogenital system in marsupials, I have consulted Mackenzie (1919), and for the female system—Pearson (1944, 1945, 1946) and Mackenzie (1919).

Three pouches or cavities (recto-vesical, recto-uterine and utero-vesical) and their related folds of peritoneum, are described in this section. In ventral dissection of an animal these were collapsed and so at first did not appear as obvious as is suggested by the following description. Details of their size and shape given here are maximum values, obtained by stretching, without damage, the peritoneal folds, thus restoring them and the pouches to what was probably their maximum living extent.

a. What is the rectum?

From Cunningham's introductory remarks on the human rectum (1937, p. 617), from his discussion on its peritoneal relations (p. 620) and from Gray's remarks on the mesocolon of the sigmoid colon (1916, p. 1103), it is apparent that the rectum is part of the hind-gut which lacks a supporting mesentery mesocolon.

Mitchell (1916) on occasion uses "rectum" to cover that part of the gut distad to the end of the pendant loop (end of right proximal colon).

In this paper the point where the mesocolon terminates is taken as the cephalic end of rectum. Here the process is begun which leads ultimately to the ventral wall of the rectum alone being covered with peritoneum. The caudal end of rectum is marked by its junction with urogenital system to form cloaca.

b. Course of rectum.

It runs straight through pelvic cavity. Length in five specimens was 60 to 85 mm. Circumference ranges from 30 to 60 mm. the variation being dependent on the quantity of faecal matter.

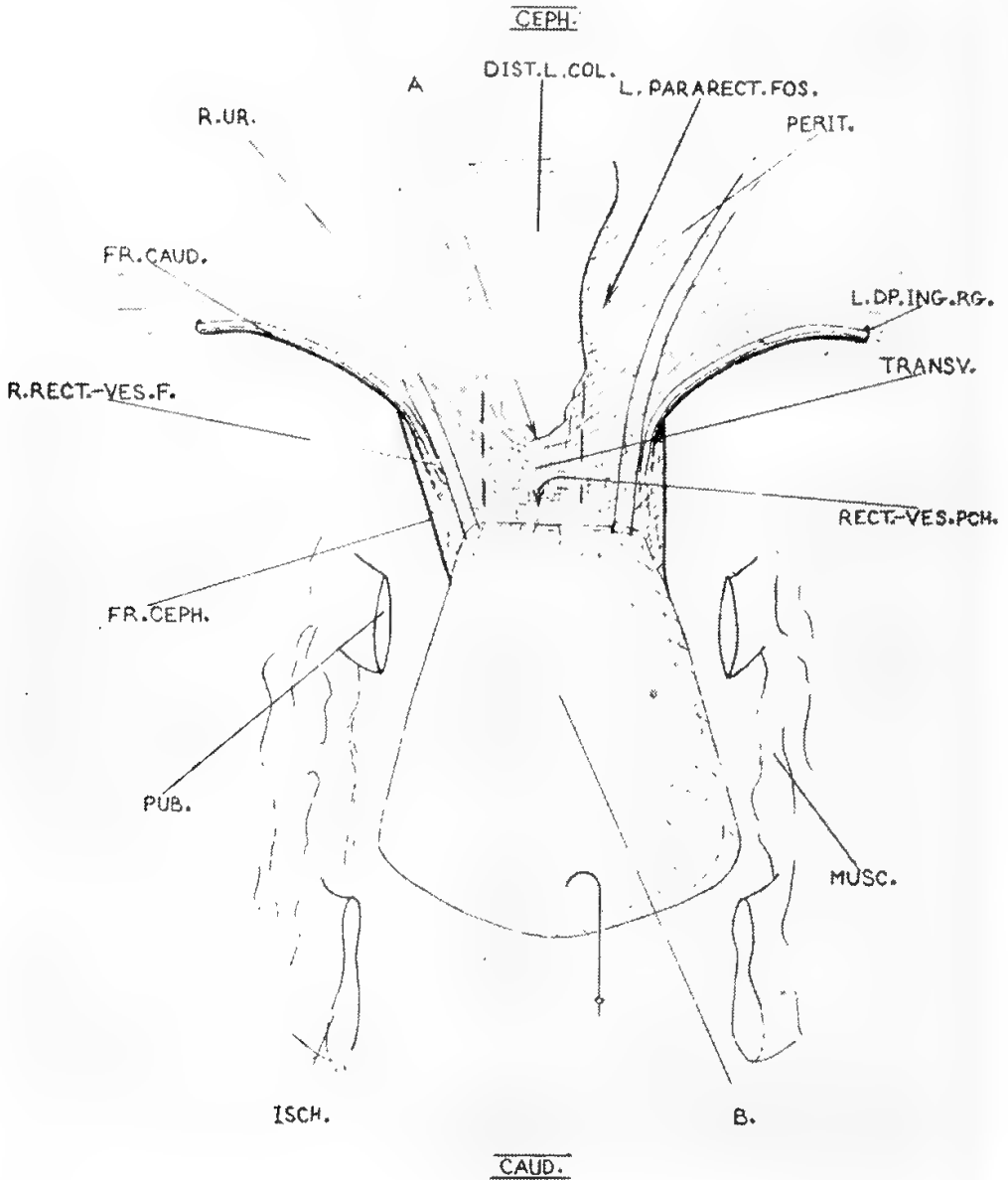
c. Support of rectum within pelvic cavity.

i. Loss of mesocolon in both sexes.—It has been indicated that the mesocolon supporting distal part of left colon within the greater (false) pelvis, narrows as colon approaches cavity of lesser (true) pelvis, i.e. as it approaches the cavity of lesser pelvis, the mobility of distal part of left colon is reduced (text fig. 29). In the region of inlet of lesser pelvic cavity and through the space of from 5 to 15 mm., the mesocolic support of left colon is lost. Mesocolon becomes detached from the dorsal, and later from the lateral, walls of rectum

which finally, in the cephalic part of the lesser pelvic cavity, has peritoneum applied merely to its ventral wall. Thus, as Cunningham (1937, p. 620) has pointed out in describing the human rectum, because only its ventral wall has peritoneum applied to it, it lies dorsal to the peritoneum. Thus rectum does not project far into peritoneal cavity.

- ii. Introduction on peritoneal adhesions within the pelvis.—For the greater part of the abdomen, the various components of the viscera, though in close contact, and despite peritoneal adhesions and supports, retain some measure of mobility. However the volume of the body cavity decreases caudad, the pelvis being a “bottle neck” to the outlet of the digestive, urinary, and genital system. The representatives of these three systems have some freedom of movement within the greater, but in the lesser pelvic cavity, they are all closely adherent to each other, so that within it there appears to be but one “visceral unit” (text figs. 33 and 35). In a general way, the peritoneal adhesions within the pelvic cavity of male are similar to those in female: differences do exist, these being related to differences in the structure of male and female urino-genital systems. In female, the insertion of the uteri and cephalic part of the vaginae between bladder and rectum, results in the development of an additional pair of peritoneal folds.
- iii. Pelvic peritoneal folds in male (text figs. 32 and 33).—Rectum and distal part of left colon lie in the dorsal portion of the lesser and greater pelvic cavities respectively. Ventral to distal part of left colon and rectum is the urogenital system, the bladder being largely in the cavity of the greater and the urethra in that of the lesser pelvis (text fig. 33).
 - (a) Recto-vesical fold. As peritoneum, following the loss of a distinct mesocolon, loses its adhesion to lateral walls of first 10 mm. of rectum, so as to finally cover its ventral wall alone, it is reflected ventrad on the right, and left sides of rectum to dorso-lateral aspect of bladder. The effect of this reflection is to produce two vertical longitudinal bands, which support bladder. They are thought to be homologous with the right and left recto-vesical folds of human anatomy (Gray, 1916, p. 1073). The reflection from sides of rectum finally becomes transverse to its ventral wall, so that, at their caudal ends, a few millimetres cephalad to beginning of prostatic urethra, the right and left recto-vesical folds may be regarded as converging and becoming continuous (text fig. 32). These bands, when stretched and viewed from the side, are broadly speaking, of triangular shape, with apex of triangle pointing caudad. Thus the bands become narrower towards their caudal ends, this narrowing being associated with the close approximation of caudal end of bladder to rectum.

Each band may be considered to have three margins—two attached and one free.



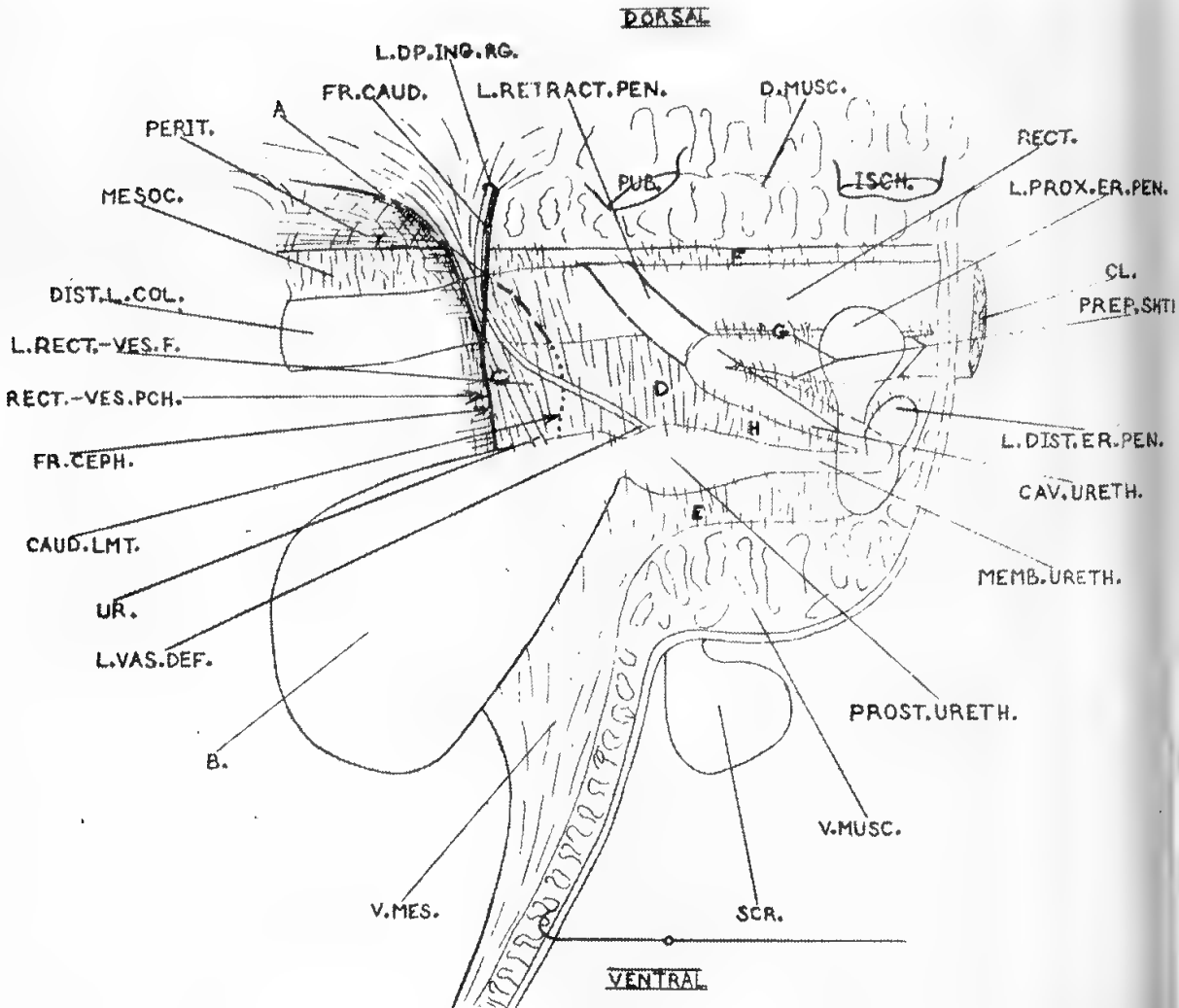
Text fig. 32.—*S. brachyurus*. Ventral view of viscera of cephalic part of pelvic cavity in the male. Ventral portion of right and left pubis and ischium removed and bladder pulled caudad into lesser pelvic cavity covering the urethra. About natural size.

At A—mesocolon becoming detached from dorsal and lateral walls of the rectum; B—distended bladder; CAUD.—caudal end of pelvic cavity; CEPH.—cephalic end of pelvic cavity; FR.CAUD.—free caudal margin of right “inguinal fold” (which arises from right recto-vesical fold) with vas deferens running through it; FR.CEPH.—free cephalic margin of right recto-vesical fold; ISCH.—ischium (cut); L.DP.ING.RG.—left deep inguinal ring (internal abdominal ring); L.PARARECT.FOS.—left para-rectal fossa; MUSC.—muscles (cut); PERIT.—peritoneum lining greater (false) pelvic cavity; PUB.—pubis (cut); R.RECT.-VES.F.—right recto-vesical fold; RECT.-VES.PCH.—recto-vesical pouch; TRANSV.—reflection of peritoneum covering ventral wall of rectum in a vertical transverse plane; UR.—ureter. Other abbreviations—see text figs. 18a and 20.

- (i) An attached margin represented by line of reflection of peritoneum from lateral and ventral walls of rectum.
- (ii) An attached margin represented by line of adhesion of recto-vesical fold to dorso-lateral walls of bladder. Cephalic end of this margin is about 40 m.m. from cephalic end of bladder.
- (iii) A free cephalic margin, 20-25 mm. long, forming third side of triangle.

On the right and left sides of greater pelvic cavity, in the region of the brim of pelvis, is a fold of peritoneum, continuous with peritoneum lining greater pelvic cavity, and also with dorsal half of free margin of corresponding recto-vesical fold. Plane of each fold is horizontal and therefore at right angles to that of the recto-vesical fold (text figs. 32 and 33). Each, extending into the corresponding inguinal region, appears to be a lateral (inguinal) extension of recto-vesical fold, having a slightly concave free caudal margin, 20-30 mm. long and stretching from free cephalic margin of recto-vesical fold to the deep inguinal ring (or internal abdominal ring). Vas deferens of each side, after emerging from the inguinal canal into pelvic cavity, runs along the free caudal margin of the corresponding inguinal fold before turning to travel caudad through recto-vesical fold to prostatic urethra. Ureter in the last 30 mm. of its course to bladder, runs through recto-vesical fold near its free cephalic margin.

- (b) Recto-vesical pouch. A cavity, which appears to be homologous with recto-vesical pouch of human anatomy (Cunningham, 1937, p. 621; recto-vesical excavation of Gray, 1916, p. 1072), lies between ventral wall of rectum and dorsal wall of bladder, and is bounded laterally by the recto-vesical folds (text fig. 32). It has been indicated that with the narrowing of the recto-vesical fold caudad, the bladder, towards its caudal end, is more closely applied to ventral wall of rectum. The effect of this, coupled with the final reflection in a vertical transverse plane of the peritoneum covering ventral wall of rectum (see p. 129), and the extensive connective tissue adhesions between distal parts of rectum and urogenital system (see later p. 138) is to reduce and finally close the cavity of the recto-vesical pouch caudad (text fig. 32). Recto-vesical pouch opens at its cephalic end into abdominal cavity by a mouth bounded by ventral wall of rectum, dorsal wall of bladder, and laterally by free cephalic margin of recto-vesical fold (text fig. 32). This mouth has a transverse width of 20-25 mm. and a dorso-ventral depth of 20-30 mm. Recto-vesical pouch has a cephalo-caudal length of about 10 mm., its caudal (blind) end being about 5 mm. anterior to cephalic end of prostatic



Text fig. 33.—*S. brachyurus*. Left lateral view of pelvic viscera of the male. Ventral portion of left pubis and ischium removed. Portion of ventral body wall has been pulled caudad and is shown in a vertical plane. $\frac{2}{3}$ natural size.

CAUD. LMT.—caudal blind end of recto-vesical pouch; CAV. URETH.—cavernous urethra; D—connective tissue between cavernous urethra and ventral wall of rectum; DIST.ER. PEN.—distal erector penis; DIST.L.COL.—caudal end of distal left colon; D.MUSC.—cut muscles of dorsal pelvic wall; E—connective tissue between urethra and ventral wall of pelvis; F—connective tissue between rectum and dorsal wall of pelvis; FR.CAUD.—free caudal margin of left “inguinal fold” with vas deferens running along it; FR.CEPH.—free cephalic margin of left recto-vesical fold; G—connective tissue between distal cavernous urethra plus preputial sheath, and ventral wall of rectum; H—connective tissue between membranous and proximal part of cavernous urethra; L.DP.ING.RG.—left deep inguinal ring (internal abdominal ring); L.ISCH.—left ischium (cut); L.PROX.ER. PEN.—left proximal erector penis; L.PUB.—left pubis (cut); L.RETRACT. PEN.—left retractor penis; L.UR.—left ureter; MEMB.URETH.—membranous urethra; MESOC.—narrowing mesocolon; PREP.SHTH.—preputial sheath; PROST.URETH.—prostatic urethra; V.MES.—“ventral mesentery”; V.MUSC.—cut muscles of ventral pelvic wall. Other abbreviations—see text figs. 10, 12, 20 and 32.

urethra, and 50-60 mm. from cephalic end of cloaca (text fig. 33).

- (c) Pararectal fossa (text fig. 32). Recto-vesical pouch extends dorsad on either side of beginning of rectum or end of left colon, to form what appears to be the rather ill defined homologue of the pararectal fossa of human anatomy (Gray, 1916, p. 1073); Cunningham, 1937, p. 621).
- iv. Pelvic peritoneal folds in the female (text figs. 34 and 35). As in male, rectum and distal part of left colon lie in dorsal portion of lesser and greater pelvic cavities respectively. Uteri, the caudal half to two-thirds of which are in contact along middle line (text fig. 34), and cephalic end of lateral vaginac and median vagina, lie ventral to distal end of left colon and proximal end of rectum. Ventral to uteri is bladder; urethra is ventral to median vagina. Urino-genital sinus is in caudal part of lesser pelvic cavity and ventral to caudal part of rectum (text fig. 35).

By the same process and through about the same space as described for male, the mesocolon, in the region of brim of pelvis, just dorsal to cephalic end of contact between right uterus and left, loses its identity (text fig. 35). Peritoneum no longer adheres to dorsal and lateral walls of cephalic part of rectum, but merely covers a portion of its ventral wall.

- (a) Recto-uterine fold (text fig. 34). In losing adhesion to rectum, the peritoneum is reflected from right and left edges of its ventral wall to dorsal wall of caudal part of right and left uterus, and thus two vertical longitudinal bands of peritoneum are produced which appear to be homologous with the right and left recto-uterine folds of human anatomy (Gray, 1916, p. 1169; Cunningham, 1937, p. 740).

Caudad, as in male, the reflection becomes transverse to ventral wall of rectum, so that, at their caudal ends, the right and left bands may be regarded as converging and becoming continuous.

Each recto-uterine fold is continuous with the broad ligament, which arises as a reflection of peritoneum lining dorsal wall of greater pelvic cavity, rather than as a fold of peritoneum covering ventro-lateral walls of rectum (cf. recto-uterine folds) (text figs. 34 and 35).

Mackenzie (1919, p. 25), in describing the general plan of the broad ligament in marsupials, states that it suspends "... the ovary, fimbriated apron, oviduct and uterus, together with the commencement of the urino-genital canal." In *Setonix* the broad ligament, beyond its attachment to ovary, extends a considerable distance up into the abdominal cavity. This extension has a free cephalo-ventral margin.

In this paper recto-uterine folds are considered to extend along uteri as far as the cephalic end of contact between uteri. Here the broad ligaments, with which the recto-uterine folds are continuous, are considered to begin (text fig. 34).

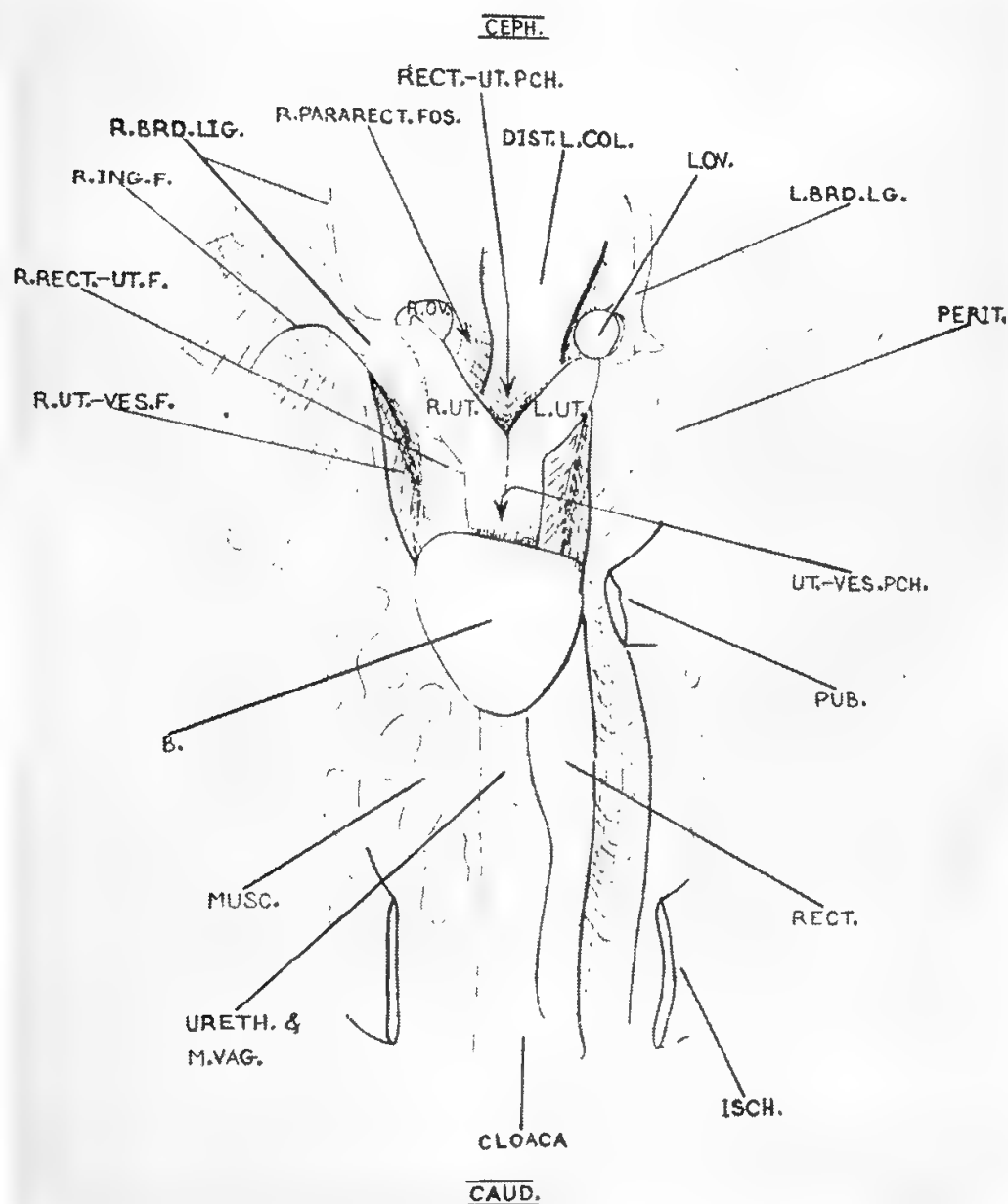
Thus, in being continuous with the broad ligaments, recto-uterine folds, unlike recto-vesical folds of male and utero-vesical folds of female (described later), have no free cephalic margin. Each has two attached margins, represented by the line of reflection of peritoneum from rectum, and by the line of its adhesion to right and left uterus.

Recto-uterine folds appear to serve as supports for caudal end of ends of uteri. This is an addition to that provided by the broad ligament.

- (b) Recto-uterine pouch. A cavity lies between ventral wall of rectum and dorsal walls of caudal ends of uteri, and is bounded laterally by the recto-uterine folds. This appears to be the homologue of the recto-uterine pouch of human anatomy (Gray, 1916, p. 1072; Cunningham, 1937, p. 621).

As the genital system approaches the more confined space of lesser pelvic cavity from greater pelvic cavity, it becomes less mobile and lies closer to rectum. The effect of this, combined with the final reflection, in a vertical transverse plane, of peritoneum covering ventral wall of rectum (see p. 133) and the extensive connective tissue adhesions between distal parts of rectum and genital system, is to reduce and close the cavity of the recto-uterine pouch caudad. Pouch opens into abdominal cavity by a mouth at cephalic end of contact between uteri, bounded by ventral wall of rectum, dorsal wall of bladder, and, laterally, by the continuous structures formed from recto-uterine folds and broad ligaments (text fig. 34). Mouth has a transverse width of about 10 mm. and a dorso-ventral depth of about 15 mm. Pouch has a cephalo-caudal length of 13-20 mm. Its blind end is about 40 mm. from cephalic end of cloaca.

- (c) Pararectal fossa (text fig. 34). Female, like male, has a right and left pararectal fossa developed on either side of rectum, as dorsal extensions of recto-uterine pouch. In the specimens examined, the fossae were not well marked. They lie on either side of distal part of left colon and beginning of rectum, and become less distinct as the peritoneum, supporting distal part of hind-gut, moves from its dorsal to its ventral side. Each fossa is bounded laterally by the broad ligament of uterus.
- (d) Utero-vesical fold (text figs. 34 and 35). Arising on each side of pelvic cavity as a reflection of recto-uterine fold and caudal half of broad ligament, and extending to



Text Fig. 34.—*S. brachyurus*. Ventral view of viscera of greater and lesser pelvic cavities of the female. Ventral portion of right and left pubis and ischium removed. The cephalic end of bladder (empty) has been pulled caudad into lesser pelvic cavity. Natural size.

CAUD.—caudal end of pelvic cavity; CEPH.—cephalic end of pelvic cavity; M.VAG.—medium vagina R. & L.BRD.LIG.—right and left broad ligaments; R.ING.F.—right inguinal fold of broad ligament (left not shown); R. PARARECT.FOS.—right pararectal fossa R.RECT.-UT.F.—right recto-uterine fold; RECT.-UT.PCH.—into recto-uterine pouch; R.OV.—right ovary; R. & L.UT.—right and left uterus; R.UT.-VES.F.—right utero-vesical fold; URETH.—urethra; UT.-VES.PCH.—into utero-vesical pouch. Other abbreviations see text figs. 18a, 20, 29 and 32.

dorsal wall of bladder, is another vertical fold of peritoneum, which, as it arises from the recto-uterine fold and not from the peritoneum investing uterus, is not strictly *utero-vesical*. The line of its reflection is roughly midway between the reflection of the broad ligament and recto-uterine fold from dorsal wall of pelvic cavity and ventral wall of rectum respectively, and their adhesion to uterus (text fig. 35).

Each utero-vesical fold is roughly triangular, apex of triangle pointing caudad. Thus the fold narrows towards its caudal end, and at the same time the bladder gets closer to the genital system.

Each utero-vesical fold may be considered to have three margins—

- (i) An attached margin represented by the line of reflection of fold from broad ligament and recto-uterine fold.
- (ii) An attached margin represented by line of adhesion of fold to bladder. The attachment ends 15 to 21 mm. from cephalic end of bladder.
- (iii) A free cephalic margin, between 20 and 30 mm. long, forming third side of triangle.

Cephalic end of reflection of each utero-vesical fold from the corresponding broad ligament and recto-uterine fold, is about 10 mm. anterior to cephalic end of adhesion of utero-vesical fold to bladder (text fig. 35). Thus the free cephalic margin of utero-vesical fold runs ventrad and caudad from the reflection from broad ligament and recto-uterine fold.

Utero-vesical folds apparently form dorsal support of bladder.

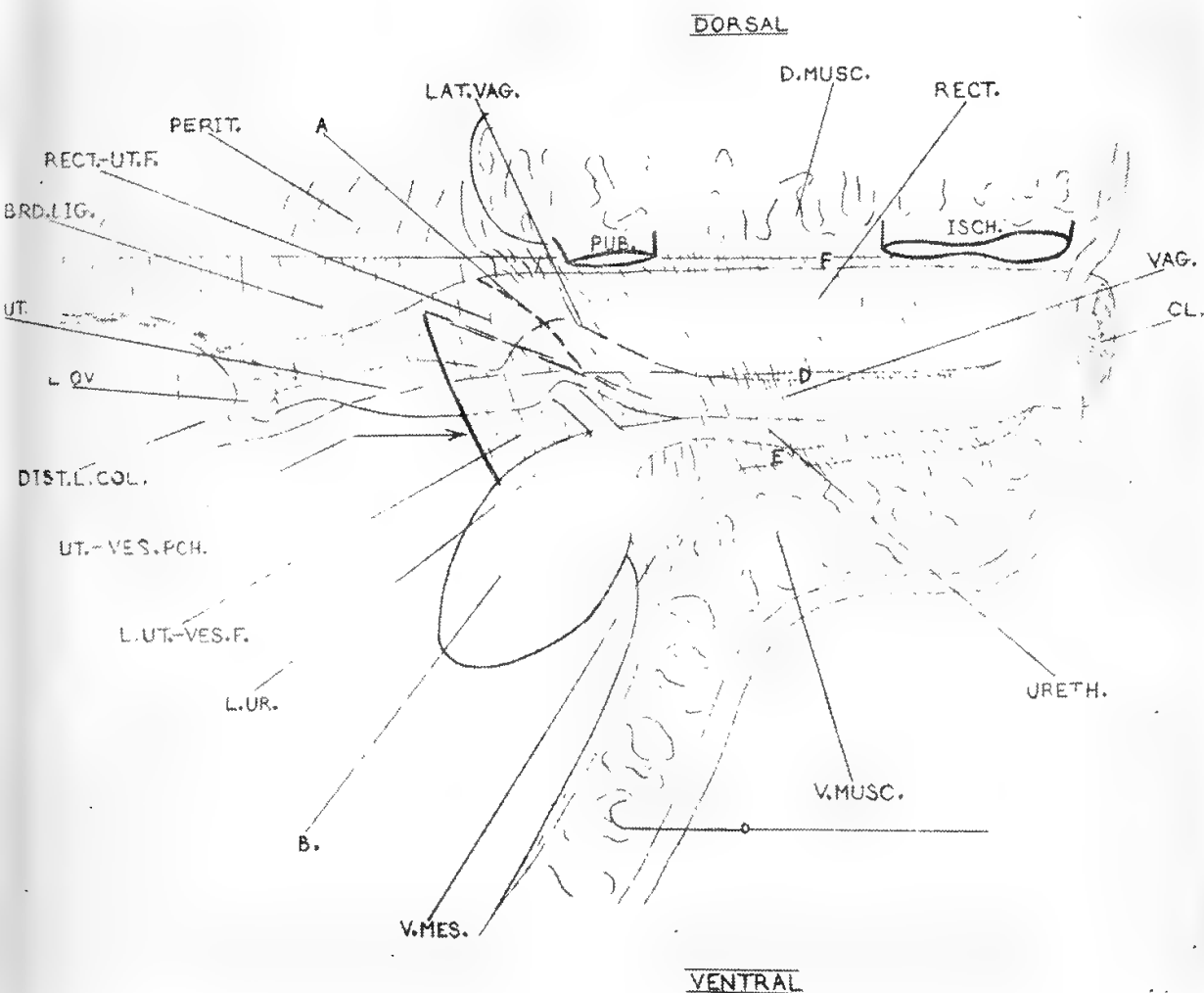
- (c) Utero-vesical pouch (text figs. 34 and 35). There is a cavity between ventral walls of caudal ends of uteri and those of cephalic ends of lateral vaginae and median vagina, and dorsal wall of bladder. It is bounded laterally by utero-vesical folds and appears to be the homologue of utero-vesical pouch of human anatomy; (Cunningham, 1937, p. 701). Through the growth of connective tissue, caudal end of bladder and urethra are close to median vagina. Thus the cavity of utero-vesical pouch is reduced and finally closed caudad (text fig. 35). It opens at its cephalic end into abdominal cavity by a mouth bounded by ventral walls of uteri, dorsal wall of bladder, and laterally by the free cephalic margins of utero-vesical folds (text fig. 34). Mouth has a transverse width of between 8 and 19 mm. and a dorso-ventral depth of between 8 and 17 mm. Pouch has a cephalo-caudal length of between 13 and 18 mm.,

its blind end being 33 to 40 mm. from cephalic end of cloaca.

Terminal part of ureter in female runs through recto-uterine and utero-vesical folds to bladder (text fig. 35).

- v. Preliminary note on ventral peritoneal fold ("ventral mesentery") in males and females (text figs. 33 and 35).

In both male and female there is a prominent vertical fold of peritoneum extending from ventral wall of bladder to ventral body wall, along which it extends some distance from the pelvic into the abdominal cavity. Together with recto-vesical folds in male and utero-vesical folds in female,



Text Fig. 35.—*S. brachyurus*. Left lateral view of pelvic viscera of female. Ventral portion of left pubis and ischium removed. Portion of ventral body wall has been pulled caudad and is shown in a vertical plane. Natural size.

At A—mesocolon becoming detached from dorsal and lateral walls of rectum; D—connective tissue binding urogenital system to rectum; E—connective tissue binding urogenital unit to ventral pelvic wall; F—connective tissue binding rectum to dorsal pelvic wall; L.RECT.-UT.F.—left recto-uterine fold; L.UT.-VES.F.—left utero-vesical fold; LAT. VAG.—lateral vagina (broken line); VAG.—caudal end of vaginal system (medium vagina and lateral vaginae closely bound together). Other abbreviations—see text figs. 10, 18a, 20, 29, 33 and 34.

it helps to retain the bladder in position. The folds may be imagined to have three margins—

- (a) An attached margin, represented by the line of reflection of peritoneum from ventral wall of bladder. Its cephalic end 10 to 30 mm. from cephalic end of bladder.
- (b) An attached margin, represented by line of reflection of peritoneum from ventral body wall.
- (c) A free, concave, cephalic margin, which, owing to the cephalic end of (b) being well in advance of the cephalic end of (a), runs cephalo-ventrad from bladder to ventral body wall.

Ventral fold of peritoneum has a maximum width of 45 mm.

vi. Relations of caudal part of rectum.

- (a) Male (text fig. 33). Termination of mesocolon with beginning of rectum does not imply that it lacks dorsal support, for along its entire length it is held to dorsal wall of lesser pelvic cavity by connective tissue. The caudal 50 to 60 mm. of rectum, i.e., of the rectum caudal to end of recto-vesical pouch, has, in addition, connective tissue extending between it and the *lateral* walls of the lesser pelvic cavity.

Stretching between the cephalic 10 to 15 mm. of rectum and bladder, are the recto-vesical folds. These arise rather from the ventro-lateral than the ventral aspect of rectum (see p. 129). Ventral wall of this part of rectum is covered with peritoneum, which is not reflected to the bladder.

With the narrowing of the recto-vesical fold as rectum and caudal part of bladder approach the confined space of the lesser from the greater pelvic cavity, the bladder becomes more closely applied to ventral wall of rectum and connective tissue adhesions develop between them (see p. 131). The various sections of the urethra are firmly bound to ventral wall of rectum so as to give the impression that there is but one "visceral unit" within the pelvic cavity.

The prostatic and cavernous urethrae are close to ventral wall of rectum. The cavernous urethra is bent into a V-shape with a longer proximal and shorter distal arm, tightly bound together by tough connective tissue. Apex of the V points cephalad. Proximal arm of cavernous urethra has connective tissue extending ventrad from it to the membranous urethra (text fig. 33). Distal arm is closely bound to ventral wall of rectum. Preputial sheath, enclosing the glans penis, is bound by connective tissue to ventral wall of rectum. (For details of male genital system in Marsupials see Mackenzie 1919, pp. 81-100).

Urethra is also bound to ventral wall of lesser pelvic cavity by connective tissue.

Retractors penis leave cavernous urethra at the apex of its V and extend cephalo-dorsad over each side of middle part

of the rectum, to which they are closely bound by connective tissue.

On right and left sides of caudal end of rectum, just before the beginning of cloaca, is a proximal erector penis. Distal erector penis, being smaller and not extending so far dorsad as the proximals, are not so closely related to rectum.

- (b) Adhesions in female (text fig. 35). Rectum in female, as in male, is bound along its entire length to dorsal wall of lesser pelvic cavity by strands of connective tissue. Caudal 40 mm. of rectum, i.e. rectum caudal to blind end of recto-uterine and utero-vesical pouches, has connective tissue extending between it and the lateral walls of pelvic cavity.

Stretching between cephalic 10 to 20 mm. of rectum and uteri, are the recto-uterine folds, and, associated with them are the utero-vesical folds. Recto-uterine folds arise as reflections of peritoneum covering ventro-lateral walls of rectum (see p. 133). Ventral wall of this cephalic part of rectum is covered with peritoneum, which is not reflected to bladder. With the narrowing of recto-uterine folds, as rectum and caudal parts of uteri approach the confined space of the lesser from the greater pelvic cavity, the uteri become more closely bound to rectum and connective tissue adhesions develop between them (see p. 134). Utero-vesical folds also narrow caudad, so that caudal part of bladder becomes closer to the median vagina (see p. 136). Urethra is bound to median vagina by connective tissues (see p. 136). Through the last 40 mm. rectum is closely bound, first to vaginal system and then, farther caudad, to urogenital sinus.

Genital and urinary systems, before their junction to form the urogenital sinus, are closely bound together. Urethra and median vagina form a unit, which, with the urogenital sinus, is bound by connective tissue, not only to ventral wall of rectum, but to lateral and ventral walls of lesser pelvic cavity.

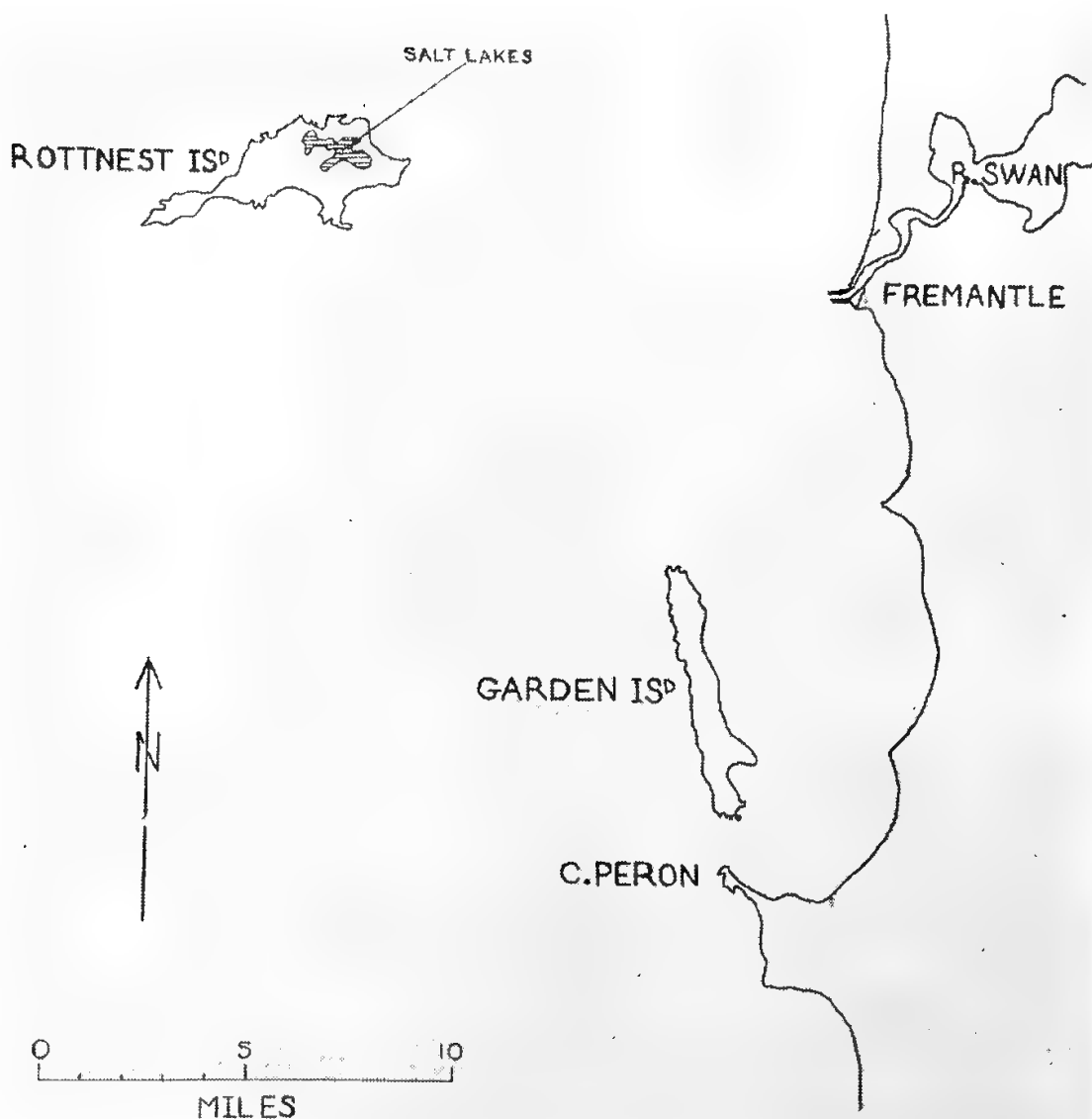
- d. Conclusion on rectum and preliminary note on uro-genital genital system of an adult female *Setonix*.

From the preceding description it can be seen that, within the cavity of the lesser pelvis in both male and female, digestive and urogenital systems are closely applied to each other, forming a compact mass and giving the appearance of being but one "visceral unit."

Connective tissue binds this unit to the dorsal, lateral, and ventral walls of lesser pelvic cavity, so that rectum and urethra in male, and rectum, vaginae, urethra, and urogenital sinus in female, are extremely immobile. This contrasts with the contents of the greater pelvis cavity, which by comparison, have much more freedom of movement, but whose mobility decreases

as they approach the cavity of the lesser pelvis. Brief examination of the genital system of one adult female showed that—

- i. Lateral vaginae were 35 mm. long.
- ii. Urogenital sinus, formed at point of coalescence of lateral vaginae (i.e. no post vaginal sinus) was 18 mm. long.
- iii. Urethra was 15 mm. long.
- iv. Caudal end of bladder is attached about halfway along the median vagina.



Text fig. 36.—Map showing relative positions of Rottneest and Garden Islands, and Cape Peron.

IV. NOTES ON NATURAL HISTORY OF THE QUOKKA.

A. THE SEPARATE OCCURRENCE OF *Macropus eugenni* ON GARDEN ISLAND AND OF *Setonix brachyurus* ON ROTTNESST ISLAND.

(Text fig. 36.) (N.B.: Glauert, 1920, p. 45 "Summary.")

Both species are recorded from the mainland of Western Australia (Shortridge, 1909, pp. 812-813; Glauert, 1934, p. 32). At present they are rare on the Swan Coastal Plain.

M. eugenni occurs in large numbers on Garden Island, south of Fremantle, and *S. brachyurus*, though not recorded from Garden Island, is equally abundant on Rottnest Island, west of Fremantle. Early French naturalists described an animal 65 cm. high from Rottnest in addition to a rat-like form: the former has been regarded as *M. eugenii*, the latter as *S. brachyurus*. Shortridge (1909, p. 813) recorded *M. eugenii* from Rottnest, but it has been suggested to me that his and the French naturalists's identifications were incorrect and that *M. eugenii* has never existed on Rottnest; it certainly does not seem to be extant on Rottnest now. Glauert (1934, p. 32) does not record *M. eugenii* or *M. derbianus* (probably really a sub species of *eugenii*), from Rottnest. If it was once present on that island, why should it have perished and *Setonix* have survived?

Rottnest and Garden Islands are both fairly well isolated from the mainland—Rottnest, the long axis of which runs east and west, being $11\frac{1}{2}$ miles, and Garden Island, which trends north and south, being only a little more than a mile offshore at its nearest point (text fig. 26). The environment on the islands is similar, both being characterized by absence of indigenous eucalypts, and presence of dense thickets of *Acacia*. Apart from size, Rottnest differs from Garden Island in having several salt lakes and also small areas of grassy heath. On Rottnest there was formerly a freshwater swamp, which is reported to have been drained within the last few years; also, in some places, fresh water, soaking down through the sand and limestone of which the island is composed, oozes out to form very small "soaks." It is reasonable to expect similar sources of water on Garden Island. *M. eugenii* and *S. brachyurus* might therefore be expected to live on either island.

Why is it then, that these islands, not far from the mainland nor from each other, and, according to geologists, only separated from the mainland in Recent or sub-Recent times (Clarke, Prider and Teichert, 1944, p. 285), should each, apparently, have its own particular macropod, although both forms exist on the mainland?

It is suggested that at the time when Garden Island and Rottnest formed part of the mainland, the physically inferior forms, such as *M. eugenii* and *S. brachyurus*, were driven by larger macropods from the richer land round the Swan River estuary to the poorer coastal sandhills. If so, the two forms would co-exist on the north-directed promontory formed of the cojoined Cape Peron, Garden and Rottnest Islands, *Setonix*, being physically inferior to *M. eugenii*, would migrate towards the end of the promontory (the present Rottnest), leaving *M. eugenii* in the Garden Island-Cape Peron region. Subsequently the

promontory was separated from the mainland and divided in two, Rottnest, inhabited by *Setonix*, being the remains of its northern tip, and Garden Island, inhabited by *M. eugenii* being its base.

B. METHOD OF CAPTURE AND OBSERVATIONS ON THE QUOKKA IN CAPTIVITY.

Seven specimens of *S. brachyurus* were kept alive in a large, earth-floored, open air cage at the Department of Biology in the University of Western Australia. With the exception of one specimen, which was "run down" in a fence corner, they were caught at night by Mr. N. Love, of the Rottnest Board of Control. I do not know exactly how he caught them possibly in the same way as a party of students caught a specimen of *M. eugenii* in November, 1946. Like the quokkas the "Garden Island wallabies" are fairly tame and, at night, move into the deserted settlement at Garden Island, probably from past habit, looking for scraps around the huts. By diverting the selected animal's attention with food, four persons, each carrying an electric torch, which was directed at the wallaby's eyes, surrounded and slowly approached it to within a few yards. The animal now got frightened and began to move slowly out of the circle of people, but after a short chase, with the wallaby in a confused state, it was captured. I am told that if one person directs a very powerful torch at the eyes of a quokka, a second person can approach from behind and catch the animal by the tail.

In captivity the quokka can live on a varied diet—household scraps, blue lupins (*Lupinus angustifolius*), thistle, grass and the leaves and flowers of a native wattle (*Acacia cyanophylla*) which grows round the University, were all acceptable. (Incidentally, the principal Rottnest acacias are *A. cuneata*, *A. cyclopsis*, and *A. rostellifera*).

Though usually crepuscular or nocturnal in the wild state, in captivity the animals were quite active during the day.

When feeding the quokka makes considerable use of the forelimb, which is surprisingly mobile, picking up or removing foreign matter from food with the hand and holding food to the mouth while it is eaten. Finlayson (1930, p. 51) notes a well developed power of grasp in *Macropus* (*Wallabia*) *ruficollis typicus*. Several times the caged quokkas were seen squatting on their hindquarters, with the tail tucked up between the hind limbs, its dorsal (superior) surface lying on the ground. Sometimes, with the tail in this position, the head is tucked down between the legs so that the animal is almost rolled up into a ball (see also Fleay, 1936, p. 153). When alarmed the quokka may emit a hissing sound and thump the ground with its foot (a common habit with the macropods).

C. "BIRTH HABITS" AND SUBSEQUENT EVENTS.

On 7/6/46 at 4.00 p.m. a quokka was noticed sitting in the corner of its box with its tail between its legs (the position described above), and clawing with its hands the fur near the cloacal opening. Occasionally it stopped clawing and licked the fur in the pubic region, thus forming a distinct track through the fur from the opening of the cloaca to the mouth of the pouch. While these actions were going on, there was a violent quivering of the abdomen and hindlimbs.

At 4.20 p.m. the animal, being disturbed, ceased these toilet activities, and leaving the box, began to feed. Five minutes later it had returned to its original position in the box and began further licking of the fur. During the preceding disturbance the definition of the track from cloaca to pouch was lost. The animal had now become much more nervous, concentrating less on the licking process. Clawing action was again seen, followed by a holding open of the mouth of the pouch with the hands. The mouth and inside of the pouch then apparently received toilet attention, the muzzle being thrust into the pouch. This was followed by a general toilet of the head and forearms. The forearm having been thoroughly licked and moistened, was used to rub the face.

At 4.50 p.m. the animal, after completing the toilet of the head, neck, shoulders, and thorax, came out of the box and began feeding with the other animals.

During the period in which these activities were observed, there was no sign of birth. The ground in the box was subsequently searched unsuccessfully for a pouch embryo, as, if born, it might have been dislodged from the parent. The activities were very similar to those described as "birth habits" by Fleay (1936, pp. 153-5) for the quokka in captivity. Subsequent events were interesting.

By 26/6/46 there was one surviving female; the other, present on 7/6/46, had died and its pouch was empty. At 11.30 a.m. on 26/6/46 the surviving female, believed to be the one whose toilet (birth) activities have been described, was observed with its tail between its legs, licking and clawing the region of the mouth of the pouch. It then hopped into its box and began eating something that it held in its hands. Investigation showed that the object was a well advanced pouch specimen which was still warm. The mother had begun eating the pouch embryo, the entire tail, the left hindlimb, portions of the pubic region, and the right hand being missing. Sex could not be determined owing to this damage.

Total length of this embryo, from tip of rhinarium to region of base of tail, was about 110 mm. Head 30 mm. long. Tongue was visible. Mouth, losing its circular outline, was becoming more slit-like, as in the adult. Lower pair of incisors visible. There was slight pigmentation of tip of muzzle. Rhinarium well formed, the median cleft and crescentic nostrils being obvious. Papillae of the 'mystical vibrissae' prominent and hair was visible round upper lip. Eyelashes could be seen on the upper eyelid, and the eyes, though closed, were well formed. Ears, about 5 mm. long, and dark grey. Head and body, apart from limited areas of grey pigmentation at tip of muzzle and on distal parts of hand and foot, pale pink. Only hairs visible were the mystical vibrissae, hairs around upper lip, eyelashes, and very short hairs on back of hand. Fingers and toes had the brown claws well developed. Palm of hand granular. Syndactyly, obvious. Bones of head, well ossified. Ribs, scapula, skeletal structures of fore and hind limb, and pelvis could be felt and were prominent. Thus the pouch embryo was fairly well advanced in its development. It had either died in the pouch (why then was it still warm?) and been deliberately removed by the parent, or, because of the loose attachment to the nipple, as indicated by the

mouth having become more slit-like, had been accidentally thrown out during the mothers' activities and thus killed.

If the adult specimen involved in these later observations was that whose toilet was watched on 7/6/46, then the following explanations are possible:—

(1) If, on 7/6/46 when the adult female was performing its toilet as described, a young animal (the well advanced embryo described) was born, then there is evidence of very rapid development after entry into the pouch, for it must have grown from a rather shapeless animal no more than 10 mm. ($\frac{1}{2}$ in.) long (see Fleay, 1936, p. 153) to the large pouch embryo.

Fleay (1936, pp. 154-5) shows indeed that the pouch embryo of the quokka does develop very rapidly, but, in the case he describes, the head and body had grown to $2\frac{1}{2}$ in. (about 65 mm.) in two months and was dark bluish pink in colour. In the case described here, if birth occurred on 7/6/46, the head and body of the embryo had developed to 110 mm. in 19 days and was still not markedly pigmented. Such rapid growth seems unlikely.

(2) Fleay (1936, p. 153) says of *Setonix* that only one embryo is carried in the pouch. Abbie (1941, p. 86) mentions, as occurring in marsupials in general, super-foetation and the survival of spermatozoa in the female tracts for long periods. Is it possible that on 7/6/46, despite Fleay's statement (1936, p. 153), a second embryo was born, the pouch already containing one specimen which subsequently grew to the 110 mm. form described above? After 26/6/46 the pouch was empty. If, then, an animal was born on 7/6/46, it presumably fell to the ground and was lost in the sand despite my searchings.

(3) Although no record was made of it, I may have had a rather violet chase before I caught and handled the suspected mother, twelve or more hours before it began the toilet activities. It is suggested that the animal, although it already had an embryo in the pouch, was disturbed in such a way by this excessive activity as to induce an imitation of the birth habits.

D. WORMS PARASITIC ON THE QUOKKA.

Several nematode worms were removed from dissected quokkas. They were up to 15 mm. long, 1 mm. thick, and of a pale colour. They were found in the regions of the greater omentum, mesial fold, and pelvic cavity. Small cyst-like structures, up to 10 mm. across, were also found in the greater omentum. They were hard and, when broken, appeared to be made up of a number of small tubes or cavities.

V. CONCLUSION ON WHOLE PAPER.

No inferences as to the phylogenetic position of *S. brachyurus* in the family Macropodidae have been drawn from this study of its externals and hindgut. Gregory (1910, pp. 11-12) and Pearson (1946, pp. 21 and 25) have pointed out that conclusions as to the phylogenetic position of an animal, based on the study of structures closely related

to environment (teeth, claws or hoofs, digestive system), are not as reliable as conclusions based on the study of organs not so easily affected by external conditions (brain, reproductive organs, foramina of the skull, auditory ossicles). Beddard (1908) and Mitchell (1916) have, however, drawn some conclusions regarding classification from studies of the gut pattern of animals.

Bensley (1903, pp. 151-2; p. 202) after a study of the teeth and feet of macropods (among other marsupials), assigned a certain position to *Setonix* in the family. To verify or amend his conclusions all anatomical systems should be considered. In this paper there is a short note on the urogenital system of one female (p. 139). Further work in this field, with references to Pearson's (1944, 1945, and 1946) work on the urogenital system of marsupials, should be valuable in determining the relationship of *Setonix* to other macropods.

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PLATE I.—The quokka in captivity. N.B. The white spot over the animal's (left) eye is not a "marking" of the fur, but a bare patch resulting from injury.



PLATE II.—Two captive specimens of the quokka (*S. brachyurus*). The animal on the right of the photo. is stretching for food held above it.

MARINE BIOLOGY IN WESTERN AUSTRALIA.

PRESIDENTIAL ADDRESS, 1947

By A. G. NICHOLLS, PH.D.

Read by Mr. J. SHEARER, July 8th, 1947.

INTRODUCTION

Twenty-three years ago, Professor W. J. Dakin, first President of the newly-constituted Royal Society of Western Australia, chose as the title of his anniversary address to members of the Society: "Marine Biology in Western Australia." I make no apology for selecting the same subject since my purpose is, primarily, to review the advances that have been made since 1914.

Introducing his subject, Professor Dakin put two questions: "What is Marine Biology?" and "What is the use of Marine Biology?" and I cannot do better than quote his own words (1916, p. 12) in answering these questions. "Marine Biology," he said, "is the study of the organisms of the sea, both animal and vegetable; their relation to each other, and to the ever-changing conditions of their environment." He went on "To the second question I require to say more. In the first place I plead the study of marine biology simply from the point of view of pure knowledge; from a desire to know and understand the earth and all that exists thereon. It is not generally known, I am afraid, that very many more groups of animals from the lowest to the highest are represented in the sea than on land and in the air. Very many problems of the greatest scientific importance are to be solved by the study of the sea and all that therein is. In fact it has been ably suggested that life originated in the sea, and that the saline constituents of mammalian blood indicate even now the composition of the medium once bathing the bodies of aquatic ancestors."

He made the point that the pursuit of knowledge for its own sake is adequate reason for studying marine biology, a view that would receive the support of the majority of scientists since so many of the great advances of a practical use have arisen from the chance observations of the merely curious scientific investigator; but, as he made clear, this branch of biology is closely tied up with the development of fisheries, which fact should satisfy those members of the community who wish to see science devoted to strictly utilitarian purposes.

Professor Dakin drew attention to the value of research into fisheries. Under this heading is included not only the study of fish (which involves a study of their spawning habits, growth-rate, food, migrations, and methods of capture) but also the study of numerous other organisms which may be of economic importance. These are, for example, mussels, oysters, trochus, and pearl-oysters, among the Mollusca; lobsters, crayfish, crabs, and prawns, among the Crustacea; and, of the lower forms of life, *bêche-de-mer*, sponges, and algae, all of which have an economic value, with possibilities of development on the Australian coast. In addition to the study of fisheries, which are productive, there is the application of marine biology to methods of preservation and efficient running—problems concerned with anti-fouling measures.

ADDITIONS TO THE MARINE FAUNA OF WESTERN AUSTRALIA SINCE 1914.

In proposing to give a summary of the additions to the marine fauna of this State which have been made since 1914, it was intended to provide for each group of the animal kingdom a list of references to all the works which dealt with the marine fauna. Circumstances and the time involved in such an undertaking have made this impracticable and (except for the fishes) the following summary refers only to such papers as have been published in the Journal of this Society. It cannot, therefore, be in any way complete, but must be regarded only as an indication of the work which has been done during the last twenty-odd years. A list of the publications referred to in this account will be found at the end, and reference to these papers will disclose additional works published elsewhere which have reference to our fauna. For the fishes a bibliography has been prepared which, it is hoped, more or less fulfils the original intention. This has been compiled from the entries in the Zoological Record.

PROTOZOA

Little work has been done on this phylum, of which the best-known marine representatives are the Foraminifera. In a paper by Chapman and Parr (1935) dealing with a series of bottom samples taken from soundings in the Bight by the trawler "Bonthorpe," 112 species were identified, one of which was new to science. It is difficult to discover how many of these comprise new recordings for this State.

PLATYHELMINTHES

Two workers have published accounts of parasitic forms. Goss (1941) described two new species of Trematodes and two new species of Cestodes, from local shags; and Sandars (1945) described five new species of Trematodes taken from the gills of some local fishes.

ACANTHOCEPHALA

A new species belonging to this group was described by Goss (1941) as a parasite in a shag.

ARTHROPODA

Crustacea. Ten species of Ostracods were identified by Chapman and Parr (1935) from soundings taken in the Bight.

The Copepods have been studied by three workers. Two new species of planktonic forms were described by Fairbridge (1944); two new bottom-living forms from the estuary of the Swan River were added by Thomson (1946); and the present writer (1943, 1945a, b, c) identified a number of marine forms occurring on our coasts, and added seven new species.

Thomson (1946) also described a new Amphipod, and two new Isopods from the Swan River Estuary, and an Isopod was added to the fauna by Glauert (1922).

Among the Decapods, the chief contribution was made by Balss (1935) in his account of the crabs collected by the Hamburg Museum Expedition. He referred to sixty species from this coast, two of which

Marine biological research of purely academic interest has not been undertaken in this State, since it depends on the facilities of a suitably equipped marine biological laboratory, where animals can be kept alive for observation and experiment. It is probable that the establishment of such a laboratory by the Council for Scientific and Industrial Research may fill this need within a few years.

The study of fisheries, on the other hand, although it can be greatly aided by the use of a marine laboratory, depends more directly on work done in the field. The C.S. and I.R. have initiated such work in this State, which has been in progress for several years now, and further reference will be made to it below.

In the absence of such facilities the only work of a marine nature that can be done is the identifying and recording of marine animals, and that work, which belongs to the field of systematic rather than to marine biology, has been carried on for many years by individuals interested in one or other of the many marine groups of the animal kingdom. This work plays an important part in laying the foundations for field work on fishery projects.

The work of recording our fauna may be said to have been started by the first navigators who visited our shores, especially when they were accompanied by naturalists. The record of their work, often published in such a way as to make it difficult of access, has been brought together by Mr. W. B. Alexander who was at one time on the staff of the Museum, and who was a member of this Society in its early days. He published a "History of Zoology in Western Australia" in a series of three papers which appeared in the Journal of the Natural History and Science Society of Western Australia (1914) and in the Journal of the Royal Society of Western Australia (1916, 1918). This account covers the period from the discovery of Australia up to 1840.

The early voyages were primarily exploratory, and it was not until the arrival of the Expedition from Hamburg Museum, to which Professor Dakin referred in his address, that a systematic account of the fauna of this State was undertaken. The published results of the work of this Expedition constitute a valuable contribution to our knowledge of the marine fauna of this State (*Die Fauna Südwest-Australiens*, 5 vols., 1907-1930, Jena). Of the nineteen phyla of the animal kingdom, almost all of which have marine representatives, nearly one half are reported on in this publication. In spite of this aid, there yet remains a tremendous field to be covered, for the study of which we must rely largely on our own efforts. Much time must therefore elapse before we have any thorough knowledge of our marine life, yet it is one which may well repay an intensive effort since practically all the collecting hitherto has been inshore, while the deeper offshore waters are untouched.

The recent proposal to set up a Biological Survey of Australia is a step in the right direction, and, while it is likely that the chief endeavour of such a Survey would, at first, be directed towards describing and recording the mammals and birds, it is to be hoped that all forms of animal life, marine as well as terrestrial, may eventually be included.

were described as new, and twenty-seven of which were recorded from this State for the first time. Montgomery (1921) had earlier contributed to our knowledge of the Hymenosomid crabs from the Swan River Estuary. Decapods collected by the trawler "Bonthorpe" were identified by Serventy (1937) who also (1938) added to our knowledge of the taxonomic features of the local estuarine shrimp.

Alexander (1916a, b) recorded eight species of Stomatopods known from our coast; and Glauert (1924) added another as well as recording the presence of several Decapods and what was probably a new Isopod.

Arachnida. The peculiar Arthropodan forms known as Pycnogonids were studied by Williams (1939) who described three new forms.

MOLLUSCA

In a "preliminary index" to the Molluscs of this State, Hedley (1916) listed between eight and nine hundred species, and stated that "this number will be increased perhaps fourfold when small species and those from deep water are collected." It has not been ascertained what proportion of these are marine, nor which were new to our fauna.

This group has not received very much attention since Hedley's paper was published, except for the primitive forms belonging to the Amphineura, also known as Chitons. In a series of papers, Ashby (1921, 1922, 1924, 1929), and Ashby and Cotton (1934), recorded the presence of four species hitherto unrecorded for this State, and added nine new forms to our fauna list. Cotton (1935) described a new species of Patelid Gastropod, and (1929) added five new species of Cephalopod molluscs.

BRACHIOPODA

In this interesting group of animals with bivalve shells, superficially resembling molluscs, Glauert (1922) recorded the presence of *Lingula* on our north-west coast.

ECHINODERMATA

The only contribution under this heading was the identification by Bennett of species collected by Dr. Serventy when on a trawling cruise in the Bight (1937).

PISCES

A new species of fish was described by Alexander (1917) which was related to a genus previously known only from Havana and Mauritius. Glauert (1921) identified a collection of fish made by the trawler "Penguin" off Albany, comprising twenty-five different species, several of which were recorded from our coasts for the first time. The same author (1922) added another species as a new record; and another new species was described by Serventy (1937) from the Bight.

Many of the papers dealing with our fish fauna, as with most other groups, have been published in journals other than that of this Society. A separate bibliography for the fishes is given below, which includes those contributions referred to in this section.

AVES

Although it may be a question of opinion as to whether sea birds visiting our shores should rightly be included in our marine fauna, I cannot omit drawing attention to the contributions made to our knowledge of this group in a series of papers by Glauert (1921, 1922, 1929, 1938, 1943).

Summarising this brief and, unfortunately, incomplete account of the additions to our marine fauna during the past 23 years, it appears that approximately 100 new forms have been added, half of them within the Crustacea. For reasons given above, this figure does not take into account Hedley's work on the molluscs. To anyone familiar with the classification of the animal kingdom it will immediately be apparent that only a very small proportion of the groups have been studied, but once again it should be stressed that this does not take into account works published elsewhere than in the Journal of this Society.

FISHERIES RESEARCH IN WESTERN AUSTRALIA.

In 1914, when Professor Dakin referred to the practical use of marine biology in the development of fisheries, little was known of the capacity of the seas off our coast to support a full-scale fishery. In the succeeding years the casual methods of fishing employed by various individual fishermen were continued and little, if any, research was done to discover the extent of our fishery resources, or to organise the fishery to the best advantage of the community.

Before the C.S. and I.R. formed the Division of Fisheries, most of the commercial fishing in this State was carried out by small craft, equipped only with very simple gear, and worked by small crews in estuaries and inlets, from beaches, or close inshore. In addition to this there was the truly marine fishery for snapper and jewfish, using hook and line, which operated from the three ports, Geraldton, Fremantle, and Bunbury. This fishery extended to north of Shark Bay. Trawling grounds were known to exist in the Bight, and off the north-west coast, but the Bight grounds were not being worked, while the other was known only from reports which filtered through from Japanese sources, since it had been discovered and worked by Japanese crews who took their catches to Singapore. There were indications that these might be rich grounds.

The formation of the Fisheries Division provided not only the stimulus but also the means of carrying out organised research into fishery problems. The work of the Division in its early years was directed towards surveying and developing fishery resources with special reference to the pelagic or surface fisheries, since the Commonwealth Government had earlier undertaken fairly extensive investigations into the demersal or bottom fisheries, under the direction of H. C. Dannevig, in the "Endeavour." From his work something had been learned of the Bight grounds.

The chief fishery resources of this State are primarily, of course, fish; but in addition there are valuable potential fisheries for crayfish, whales, turtles, edible and pearl oysters, sharks (for the liver oils), possibly sponges, and for those sea-weeds which yield agar-agar.

Fisheries based on bottom-living fish inhabiting clearly-defined grounds do not present any great problem. Once the grounds have been located, and provided they are of sufficient extent to support an established fishery, the problem is one of rational exploitation. Such fisheries, by virtue of their nature, require strongly-built, sea-going vessels, equipped with heavy gear and a sufficient crew. These factors all contribute to a high initial expense and relatively high running costs, so that to be a success financially, reliable supplies of fish are essential.

In the case of fish which live at or near the surface, and roam the seas in their search for food—the pelagic fish—the problem of continued supplies is much more serious, although the lower capital outlay and running costs compensate for this disadvantage to a certain extent. In the case of the European herring, which is a pelagic fish, continuity of supplies is more or less assured owing to the knowledge of their habits which fishermen have gained from generations of experience. Even in this case, supplies are not always assured, and fishermen may return to port with poor catches, so that research into the factors which control the migrations of herring has been going on for many years. Attempts have been made in Europe and in the United States to employ aircraft for spotting shoals of fish, particularly the herring, and these efforts have met with varying amounts of success. Similar work has been undertaken in Australia by the C.S. and I.R. Towards the end of 1942 work began in this State by an observer accompanying coastal patrols from which were derived much useful information, supported by aerial photographs. Later, identification of the fish composing some of the large shoals was confirmed by employing a fishing vessel to work in co-operation with aerial spotting.

The results of this survey in Western Australia, during which nearly the whole of the coast-line of the State was covered on several occasions at different seasons, enabled the observer to report the presence of large shoals of pelagic fish in local waters. It would seem, therefore, that aerial spotting of fish shoals should be a practical method of locating pelagic fish, resulting in a considerable saving of time normally spent in searching by boat. Much work, however, remains to be done to discover the best method of catching such fish once they have been located, and future research by officers of the Division may be along these lines. It is to be hoped that their efforts will meet with every success and that the fishing industry in this State will be put on a sound commercial basis.

There are, however, other fisheries of commercial value to the State, and one of these is concerned with the mullet (*Mugil dobula*). This fish spends part of its life in the sea, and part in river estuaries. It is not restricted to the west coast but occurs in the east, and this species has been the subject of research during the past few years. Much remains to be discovered about the habits of this fish, and as part of the endeavour to learn more about its migrations, an extensive programme of tagging has been undertaken.

Similar work has been done on the Perth Herring (*Nematolosa come*), and research has also been undertaken on the Australian salmon (*Arripis trutta*), more particularly in relation to its suitability for canning, since it is not highly regarded in its fresh state but yields a very attractive canned product.

The life-history, habits, distribution, and marketing of the marine crayfish are also being investigated. There are several species of this crustacean known to this State, one belonging to the genus *Jasus*, the others to the genus *Panulirus*. The Southern Commercial Crayfish (*J. lalandii*) is to be found from Cape Naturaliste south to the Leeuwin, and thence eastwards at least as far as Esperance. It is also found on the south-eastern coast of Australia, and in South Africa and New Zealand, in all of which places it is marketed though as yet there is no fishery for it on a commercial basis in this State.

The Western Australian Commercial Crayfish (*Panulirus longipes*) occurs from Cape Leeuwin northwards to Vlaming Head on North-West Cape, and possibly further north. Three other species of this genus are known to occur on the north-west coast, and appear to be associated with coral reefs or muddy grounds. The coast-line in the range of *P. longipes* has a very extensive series of reefs which harbour the crayfish, but commercial working over much of the ground is rendered difficult owing to the lack of harbours and roads so that this ground is virtually unfishable under existing conditions and may constitute a natural sanctuary which could contribute to the stock of the commercial grounds by means of larval distribution.

In conjunction with this work, hydrological investigations and studies of the plankton are being carried out, while the related question of the study of ocean currents is also being watched. From the evidence of drift-bottles there are reasons for believing that the set of currents along the west coast is not quite as simple as has been thought. This work should prove of great value in the future, since the movements and distribution of the drifting food of fish, and of the young stages of fish and crayfish, are largely governed by movements of the water. At present, however, drift-bottle work is limited to the surface.

Botanical work in this State has been undertaken on the larger algae, particularly in connection with the search for an alternative source for agar-agar, most of the world supplies of which used to come from Japan. Two suitable algae occur on our coast, *Gracilaria* and *Eucheuma*, and of these the former yields the higher grade product for bacteriological work. Unfortunately, the variety of that algae occurring here has a lower yield of agar than the similar form in the Eastern States. Only *Eucheuma* is of commercial value here, and, although it yields a product unsuitable for bacteriological purposes, it is excellent for many industrial needs.

The Natural Science Departments of the University have co-operated to some extent in the exploratory work carried out by the Division of Fisheries, and are of course undertaking research of more academic interest such as ecological surveys and the study of the seasonal succession of marine algae on shore reefs. Studies of shore ecology on the south-west coast of this State are rendered difficult by the absence of regular and predictable tides (Curlewis, 1916).

Having undertaken this attempt to bring up-to-date an account of Marine Biology in this State, it is appropriate to take stock of what has been accomplished during the past twenty-three years.

Useful academic work has been done by those who have contributed

to our knowledge of the systematics and ecology of our fauna and flora, but in these fields much remains to be done.

On the economic side, research is getting into its stride, and while much has been accomplished there is still much to be done. Co-operation between State and Commonwealth organisations in fisheries research has been whole-hearted throughout, and it is only by such co-operation that the best results will be achieved in the shortest time.

In concluding this account I would express the hope, which I am confident will be more than fulfilled, that the next quarter-century of research in marine biology in this State will yield even greater results, and that this branch of science will play its full part in the development of our natural resources.

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